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Cover: Early evidence of extinction: *in situ* tooth of extinct mastodon contrasted with that of living elephant drawn by Jan Van Rymsdyk to illustrate William Hunter's Royal Society paper of 1768 (see *Earth Sciences History*, **3**, 17, fig. 1). Reproduced by permission of the Keeper of the Hunterian Books and MSS (Glasgow University Library, Hunterian fig. 92.3).

A NEW FEATHER FROM THE LOWER CRETACEOUS OF BRAZIL

by DAVID M. MARTILL *and* J. B. M. FILGUEIRA

ABSTRACT. A semi-plume feather from the Nova Olinda Member of the Crato Formation (Aptian, Lower Cretaceous) of north-east Brazil is only the second feather reported from this remarkable lagerstätte. The new specimen is presumed to be preserved as an organic film in organic-rich, laminated limestones, and is from an unknown bird probably in the size range 150 to 300 mm.

AVIAN remains are extremely rare in the Mesozoic, so that even isolated occurrences of feathers are of interest. Although usually of little taxonomic importance, except to demonstrate unequivocally the presence of birds, the preservation of such organic structures as feathers is itself of interest. We here report on the occurrence of an isolated contour feather which is preserved as organic material, and shows relatively fine structures including the presence of barbules.

A feather was first reported from the Cretaceous of the Chapada do Araripe, Ceará, NE Brazil, by Martins-Neto and Kellner (1988) who noted the occurrence of a small flight feather from the Crato Formation (equivalent to the Crato Member of the Santana Formation of Martins-Neto and Kellner (see Martill and Wilby 1993 for full discussion of the stratigraphical nomenclature of these deposits)). This feather was later figured by Kellner *et al.* (1991). The new specimen is housed in the collection of the Department of Geology, University of Leicester, UK; No. LEIUG 114369.

This is only the third reported occurrence of avian remains from the Cretaceous of Brazil. Chiappe (1991) reported the occurrence of an avian carpometacarpus from the Upper Cretaceous Bauru Formation in addition to the feather noted above.

LOCALITY

The Crato Formation forms an arcuate outcrop on the south-eastern, eastern and north-eastern flanks of the Chapada do Araripe, in Pernambuco and Ceará, north-east Brazil (Martill 1993). The outcrop is almost continuous, and is fossiliferous in most places. The Chapada do Araripe is a plateau dominated by high sandstone cliffs of probable Cenomanian age, which overlie early Cretaceous and late Jurassic sediments. Exposures are good to excellent where streams have deeply incised the softer sediments.

The new find comes from a recently discovered locality of the Crato Formation close to the Tatajuba Reservoir some ten kilometres west of Nova Olinda (Text-fig. 1), which is the main area of commercial exploitation of the Crato Formation. This new locality, called the Mina de Antone Phillipe, is currently worked for large slabs of unweathered rock which are suitable for manufacturing table tops. The new specimen was collected by one of the quarry workers, and passed to the owner of the quarry. This was most fortunate, as the quarry lies outside the main commercial collecting area, and most fossils at this site are ignored (B. Filgueira, pers. comm.).

STRATIGRAPHY AND PALAEOENVIRONMENT

The Crato Formation is a series of finely laminated, organic-rich carbonates with intervening units of sands, silts and silty clays. Three distinct laminated carbonate units can be recognized: a lower Nova Olinda Member, the Barbalha Member and an upper Jamacaru Member (Martill and Wilby

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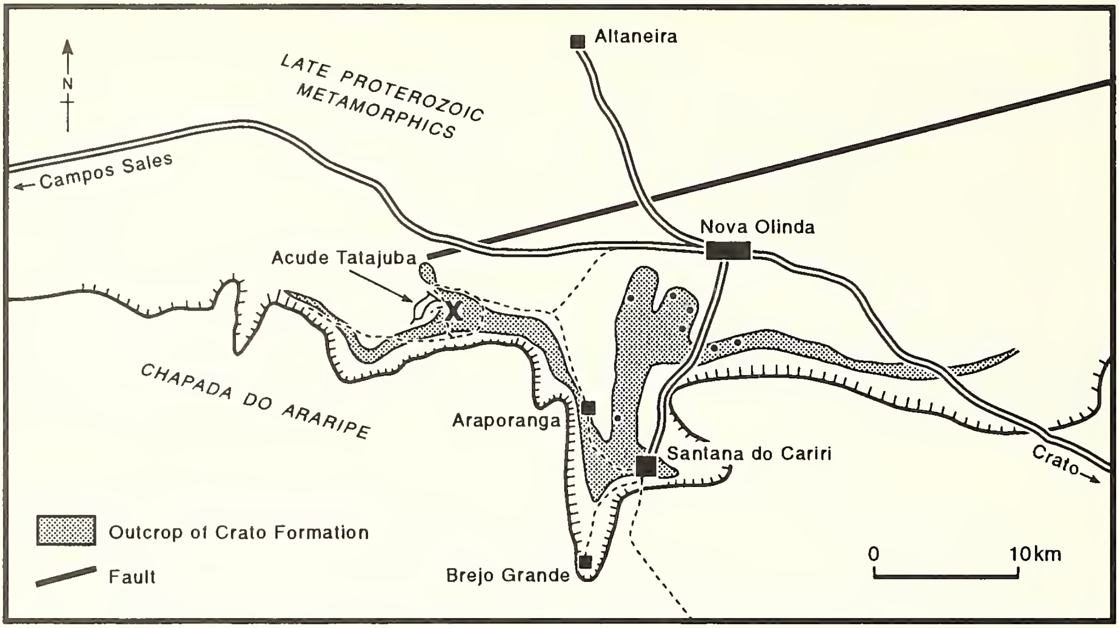


TEXT-FIG. 1. Sketch map showing the new locality in the Crato Formation where the new feather was discovered.

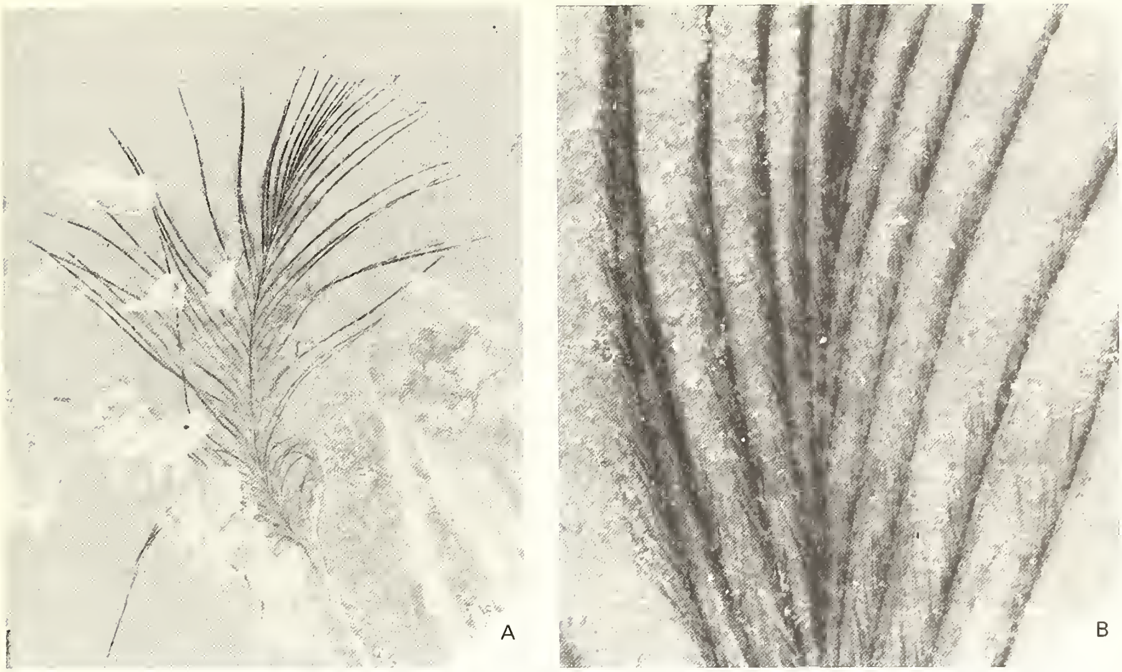
1993). The new feather comes from the Nova Olinda Member. In the region around Nova Olinda, this limestone forms a minor escarpment and is mined for ornamental stone. The mining techniques are labour intensive, and consequently many fossils, mainly the small fish *Dastilbe* and insects, are found. The Crato Formation at this locality is close to its unconformity on the underlying neo-Proterozoic basement, and was probably deposited close to the palaeoshoreline of the Crato lagoon.

The precise age of the Crato Formation is in some doubt due to a lack of diagnostic macrofossils, but palynological evidence suggests an Upper Aptian age (Pons *et al.* 1990).

The Crato Formation was deposited in a lagoon in an enclosed basin which may have had restricted access to marine waters to either the south or, perhaps less likely, to the west (Martill and Wilby 1993). The bottom waters of the lagoon were almost certainly anoxic and sulphate-reducing bacteria thrived in the bottom sediment. The surrounding region was arid (Maisey 1990) and clastic sediment input was minimal during deposition of the Nova Olinda Member. Mass mortalities of small fishes were frequent. The para-autochthonous fauna is restricted and consists of the gonorhynchiforme fish *Dastilbe elongatus* and a few insect larvae. Conchostracans are abundant at the base of the Nova Olinda Member, but they gradually disappear through the basal few metres due to a presumed increase in salinity. The most common fossils are those of animals and plants that were blown in, dropped in accidentally, or were predated while flying over the lagoon.

DESCRIPTION

The new feather is a semiplume which has been damaged somewhat since or during collection. The proximal part of the calamus is missing (Text-fig. 2A). The length of the preserved specimen is 21 mm measured along the slightly curved rachis. It has a maximum width of 18 mm, due in part to spreading of the barbs. The longest barbs are from 8 to 10 mm long. Barbules are visible on a number of barbs with both proximal and distal barbules being identifiable (Text-fig. 2B). Barbules are up to 0·04 mm long, with up to sixteen barbules per millimetre on those parts of the barbs where they can be easily counted. The feather resembles those from the posterior part of the



TEXT-FIG. 2. Photographs of the new feather; specimen number LEIUG 114369. A, the feather on a bedding plane of typical unweathered Crato Formation laminite. Nova Olinda Member, Crato Formation, Tatajuba, Ceará, NE Brazil. Notice the chisel marks, one of which has cut across the specimen; × 3·5. B, detail of the barbs and barbules in the distal region of the feather; *c.* × 35.

body of modern passerines and is comparable in size with birds of between 150 and 300 mm in length.

PRESERVATION

The feather is preserved flattened on a smooth bedding plane. A number of barbs have separated from adjacent barbs, and some are folded back towards the proximal end of the rachis. The overall colour of the feather is dark grey distally, to light grey proximally.

The first feather described by Martins-Neto and Kellner (1988) is preserved as a limonitic by-product of a weathered pyritic permineralization, a common occurrence for fossils from those parts of the intensely weathered Crato Formation which are worked for paving stone in the region of Nova Olinda. In contrast, the feather described here appears to be preserved organically, although no tests have been performed to prove this for fear of damaging the specimen further. An insect from the same locality as the new feather has been found with colour patterns preserved (Betimar Filgueira pers. comm.) and plant fossils are carbonized. Of note, however, is the greater fidelity of preservation at the new locality, as Kellner *et al.* (1991) reported that barbules are not visible in the first specimen.

The feather is remarkably similar in size, morphology, and preservation, to that figured by Talent *et al.* (1966) from the Valanginian to Aptian sequence of Koonwarra, Victoria, Australia.

OTHER OCCURRENCES OF MESOZOIC FEATHERS

Several authors have reported the occurrence of feathers from Mesozoic deposits, including some associated with skeletal remains, the most remarkable being those of *Archaeopteryx lithographica* from the Upper Jurassic of Bavaria (Ostrom 1984; Rietschel 1984). These examples still rank as the oldest undisputed avian remains. Other feathers reported from the Mesozoic include a contour feather from the Lower Cretaceous (Berriasian to early Valanginian) of Montsech, Lerida Province, Spain (Ferrer-Condal 1954), and some rather unusual, probably primitive, feathers lacking barbules from the Upper Jurassic of the Karatau Mountains, Mongolia (Rautian 1978). However, some workers consider the supposed primitive feather described by Rautian (1978) is more likely to represent a benettitalean leaf, a common fossil in the Upper Jurassic deposits of Karatau (P. Wellnhofer pers. comm.). Rather more examples have been reported from the Lower Cretaceous, with some of the finest coming from the probably Hauterivian to Aptian of Mongolia (Kurochkin 1982). Both isolated feathers and examples associated with skeletal remains are reported from this latter locality, and in some of the better examples the colour pattern (but not the original colour) is retained (Kurochkin 1985).

Recent discoveries from the early Cretaceous (Barremian) of Las Hoyas, Spain, include skeletal remains with associated feathers (Sanz *et al.* 1988; Sanz and Buscalioni 1992). Three isolated feathers have been reported from the Lower Cretaceous Korumburra Group of Victoria, Australia (Talent *et al.* 1966; Waldman 1970). Ambers from the Lower Cretaceous of Lebanon have been described with feathers as inclusions (Schlee 1973), and Upper Cretaceous ambers from Alberta, Canada have also likewise been reported with feather inclusions (E. M. Pike, pers. comm.). For a general review of Mesozoic birds see Olson (1985).

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Note added in press. Since submission of the typescript, one of the authors (DMM) and E. Frey have collected six more feathers from this locality.

FOSSIL DOWN FEATHER FROM THE LOWER CRETACEOUS OF BRAZIL

by A. W. A. KELLNER, J. G. MAISEY *and* D. A. CAMPOS

ABSTRACT. An Early Cretaceous (Aptian) fossil feather has been discovered in the Araripe Basin, northeast Brazil. Its features, including an overall fluffy aspect, indicate that it is a definitive down feather. This new material provides empirical evidence that birds had already developed an effective thermoregulatory insulation cover, with down feathers, by the Early Cretaceous. Furthermore, in the absence of skeletal remains, the fossil feathers are the only reliable evidence of Mesozoic birds in Brazil.

THE Lower Cretaceous Santana Formation of the Araripe Basin, northeast Brazil (Text-fig. 1), is very well known for the large quantity and exquisite preservation of its fossils (see Maisey 1991 for a review). The basal unit of the Santana Formation is the Crato Member, which includes laminated light gray micritic limestones alternating with dark-coloured, calcareous silty shales (Mabesoone and Tinoco 1973). According to recent palynological data the age of the Crato Member is Late Aptian (Pons *et al.* 1990). Fossils are abundant in these sediments, especially small gonorynchiform fishes (Blum 1991) and a rich and diversified assemblage of insects (Grimaldi 1990; Martins Neto 1991). Other fossils such as pterosaurs (Kellner in preparation) and turtles are more rare. The depositional environment is generally regarded as lacustrine (Beurlen 1971), which is supported by the presence of freshwater insect larvae as well as halophobic vertebrates such as anurans (Kellner and Campos 1986). The presence of volant birds was demonstrated recently by the discovery of a flight feather (Martins Neto and Kellner 1988). Another feather having a profoundly different morphology is described here. It is housed in the palaeontological collection of the Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil, as specimen DNPM MCT 1493-R.

DESCRIPTION

The feather is comparatively small, with a preserved length of approximately 7·5 mm, measured from the preserved part of the calamus to the largest barb (Text-fig. 2). Its color is dark-brown, contrasting with the greyish color of the limestone slab in which it is preserved. There is almost no difference in relief between feather and matrix, possibly due to diagenetic process. SEM pictures of the uncoated specimen did not reveal any ultrastructure or featherprint. Many identifiable structures are, however, preserved. All measurements were taken by a digital optical micrometer (Shopscope Tm and Microcode II Tm).

The shaft includes both the calamus and rachis. The calamus is weakly preserved and is represented only by a faint shadow. The rachis is very thin and is about 3·4 mm long, corresponding to approximately 46 per cent of the feather's total preserved length. Compared to the largest barbs, the rachis is smaller, which is one of the main characteristics used to distinguish down feathers from other types of feather (Lucas and Stettenheim 1972). No evidence of an afterfeather or hyporachis is observed.

The vanes are very clearly preserved. Some of the barbs are almost as thick as the rachis. The size of individual barbs decreases towards the distal portion of the shaft. The last and smallest barb on the terminal portion of the shaft is approximately 2·9 mm long, while the largest barb near the base of the shaft has a length of approximately 5·3 mm. There are approximately three to four barbs per mm of rachis. Barbules are longer on the proximal parts of the barbs. This increases the down density of the feather towards the rachis.

On the left upper portion in the matrix above the feather, a comparatively very long barb-like structure is present, at least 25 mm long, straight distally and curved proximally. Although poorly preserved, it is possible

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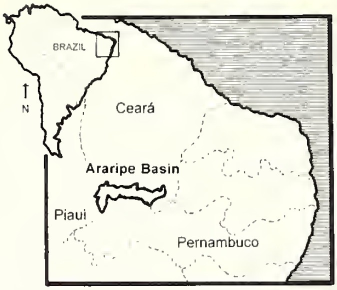
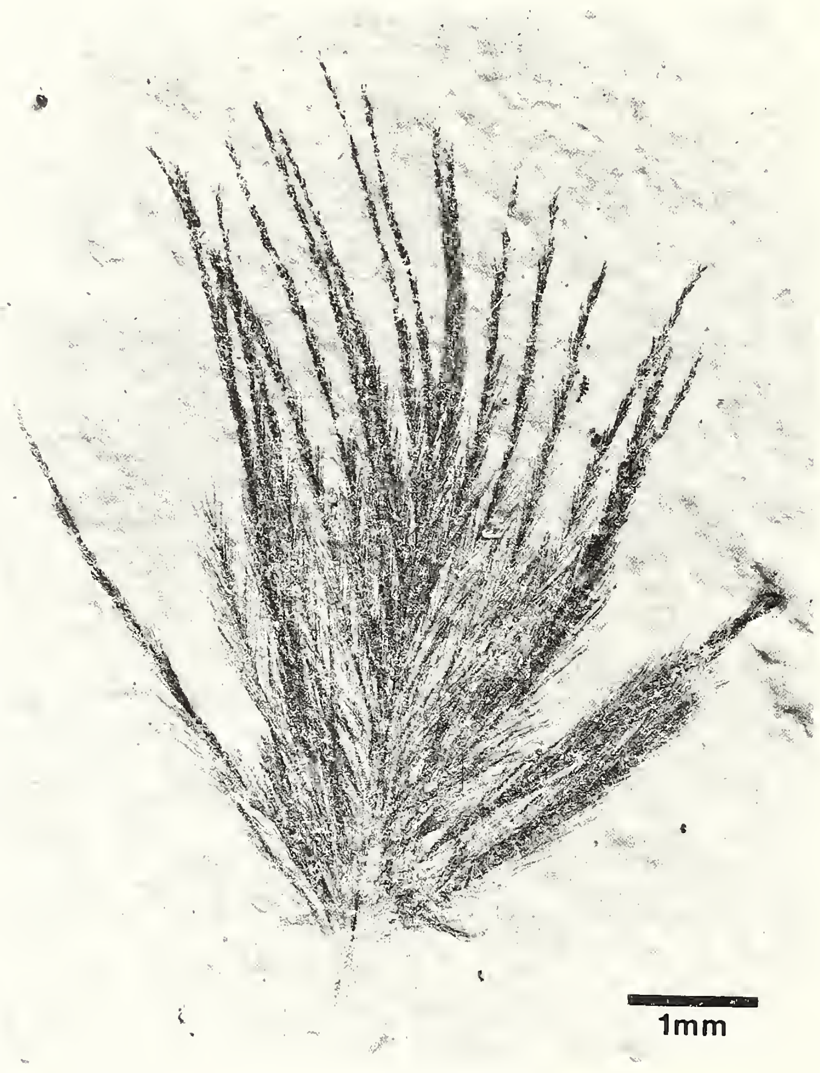


TEXT-FIG. 1. Map of South America, showing the position of the Araripe Basin.



TEXT-FIG. 2. Fossil down feather (MCT 1493-R) housed in the palaeontological collection of the Departamento Nacional da Produção Mineral (DNPM, Rio de Janeiro).

that the structure may have been connected originally with the largest basal barb. No barbules were observed on this structure, however, and it is entirely possible that it is not part of the feather.

All the above features, notably the proportional size of the rachis and the barbs, and the overall fluffy aspect of this feather, indicate that it is a definitive down feather, i.e. a feather developed only with the full body plumage (Lucas and Stettenheim 1972).

DISCUSSION

Fossil feathers are very rare in the palaeontological record, due to the fragility of their structure, and their preservation requires special fossilization conditions. Those conditions are found normally in calm waters of lacustrine (e.g. Waldman 1970; Kurochkin 1985; Martins Neto and Kellner 1988) or lagoonal environments (e.g. Meyer 1861). The best preserved feather (as well as other fossils in general) are found in amber, such as the specimen described by Schlee (1973), Schlee and Glöckner (1978), and the semiplume recently found in Lower Cretaceous deposits of New Jersey (D. Grimaldi pers. comm.).

In the Mesozoic, very few fossil feathers are known (Martins Neto and Kellner 1988; Kellner *et al.* 1991 and literature cited therein), limiting the information about primitive avian plumage. Most skeletal remains of early birds lack traces of an external body covering (e.g. Sanz *et al.* 1988; Sereno and Chenggang 1992). The reported Mesozoic feathers are contours, remiges, rectrices, or semiplumes (Martins Neto and Kellner 1988; Lacasa 1988). The only other supposed down feather reported so far comes from the Lower Cretaceous of Mongolia and was merely figured but not described (Kurochkin 1985). If it is a genuine down feather, it differs from the specimen described here in lacking a rachis (or having it greatly reduced), and by the apparent absence of barbules on the barbs.

Depending on their function, feathers have different shapes and structures. Down feathers are commonly regarded as best adapted to provide thermal insulation (e.g. Lucas and Stettenheim 1972; Gill 1990). The presence of down feathers in the Lower Cretaceous therefore suggests that bird plumage was already highly differentiated, with a wide range of functions including flight and an effective system of thermal insulation.

Although no skeletal material of birds have yet been reported from the Brazilian Mesozoic, the presence of feathers increases the expectation of finding early bird remains in this country, particularly in the Crato Member.

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MICROSTRUCTURAL ANALYSIS OF BONE OF THE SAUROPOD DINOSAUR *SEISMOSAURUS* BY TRANSMISSION ELECTRON MICROSCOPY

by THOMAS G. ZOCCO *and* HILDE L. SCHWARTZ

ABSTRACT. Transmission electron microscopy (TEM) is commonly used to characterize materials with respect to crystal structure, chemical composition, defect density and type, as well as other microstructural features. Observation of bone from the Upper Jurassic sauropod dinosaur *Seismosaurus* using this technique, reveals a unique bimodal crystallite structure which appears to have local preferred orientation. Most crystallites are small oblong grains, averaging approximately 100 nm long and 20 nm wide; larger hexagonal crystallites are also present, ranging from 80 to 400 nm in diameter. The larger crystallites are found near naturally occurring canals and pores in the *Seismosaurus* bone. Electron diffraction and chemical analyses show that both the small and large crystallites are composed of fluorapatite. Comparative analyses of *Seismosaurus* with modern crocodile, Pleistocene mammoth, and Cretaceous theropod dinosaur bones show that younger fossil bone microstructure is essentially unaltered; the older fossil bones share a unique crystalline microstructure in which original and diagenetic apatite is intermixed.

BONE is an abundant and important component of the fossil record. Historically, research on the changes that occur in bone with burial and time has focused on mineralogy and histology, which relate to fluorine dating, diagenetic, and palaeoecological studies. This work has led to recognition of some general aspects of bone fossilization, including: (1) alteration of original bone apatite, generally carbonate hydroxyapatite ($Ca_5(PO_4,CO_3)_3(Cl,OH,F)_2$) to carbonate fluorapatite ($Ca_5(PO_4,CO_3)_3F_2$); (2) selective isomorphous substitution of certain elements (e.g. fluorine, uranium, rare earth elements) and the loss of others (e.g. nitrogen) from bone mineral; (3) the gradual loss of organic matter from bone matrix; and (4) the introduction of new mineral phases into pores and interstices left vacant by the removal of organic material. It has been known for more than a century that much, if not most, fossil bone is composed of either carbonate hydroxyapatite or its isostructural counterpart, carbonate fluorapatite (Middleton 1844; Carnot 1893). However, it is not known whether fossil bone apatite is original material or recrystallized.

Along with mineralogy, the crystalline ultrastructure of fossil bone is a key to understanding how and to what extent the fossils are changed from their primary state. In modern mammal bone, the crystallite constituents of bone apatite vary in size from 10 to 400 nm in length and width and 1 to 7·5 nm in thickness (Fitton Jackson and Randall 1956; Engstrom 1960; Cameron 1972). Variation in crystallite size occurs between different species (Osmund and Sawin 1959; Tannenbaum and Termine 1965), between different bones in the same animal and in different regions of the same bone (Robinson and Cameron 1964), and within living bone with age and/or fluorine uptake (Zipkin *et al.* 1962; Robinson and Cameron 1964; Eanes 1965; Posner *et al.* 1965; Tannenbaum and Termine 1965; Simpson 1966). Scanning electron microscopy (SEM) analyses of modern mammal bone show that the crystallites are rod-, needle- or tablet-shaped (Neuman and Neuman 1958; Robinson and Cameron 1964; Cameron 1972) and are aligned more or less parallel to collagen fibrils (e.g. Fernandez-Moran and Engstrom 1957; Eanes 1965). The extremely small size of bone apatite crystallites gives them large surface areas of 100–200 m^2/g (Engstrom 1972).

Few studies have looked at the comparative physical ultrastructure of fossil bones, but Jaffe and Sherwood (1951), Osmund and Sawin (1959), Brophy and Hatch (1962), Wyckoff *et al.* (1963),

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Lozinski (1973), and Tuross *et al.* (1989) used X-ray diffraction and/or powder X-ray photography to document changes in the sizes of apatite crystallites and unit cell parameters in fossil bone. Taken together, their results are contradictory and do not establish a model for change in bone apatite with time. Wyckoff *et al.* (1963), Wyckoff and Doberenz (1965), Wyckoff (1972), Tuross *et al.* (1980), and Wyckoff (1980) recorded good preservation of both organic and inorganic bone matrix in fossils using SEM and microradiographic images.

Surprisingly, transmission electron microscopy (TEM) has rarely been employed in studies of fossil ultrastructure, despite its wide use in biological ultrastructure and materials microstructure research. TEM allows simultaneous high magnification observation and high spatial resolution chemical analyses, which is advantageous over the more common scanning electron microscopy. Most of the studies which do include TEM analysis of fossils, look at histology and organic structure (ultrastructure), rather than inorganic mineral structure (e.g. Shackleford and Wyckoff 1964; Doberenz and Wyckoff 1967; Pawlicki 1978; Towe 1980), with the exception of Wyckoff (1972).

We originally examined inorganic structure (microstructure), and composition of a well-preserved fragment of the ischium from the Jurassic of the dinosaur *Seismosaurus* of New Mexico, using TEM in order to determine the presence and/or extent of recrystallization within the bone, and thus determine its degree of originality. *Seismosaurus* is a large sauropod dinosaur recently described by Gillette (1991). It belongs to the Diplodocidae and is known from the partial skeleton of one individual recovered from the Brushy Basin Member of the Morrison Formation (Schwartz and Manley 1992). The unexpected and unusual ultrastructure of *Seismosaurus* bone led us to a comparative examination of three other samples: a limb bone fragment from the Cretaceous theropod dinosaur, (probably *Albertosaurus*) (from Alberta, Canada); a limb fragment from a Late Pleistocene mammoth (from central Utah); and a scute from a recent crocodile (from Kenya) (Table 1). The theropod and crocodile specimens were collected and identified by the second author; the mammoth bone was collected and identified by D. D. Gillette. These specimens were chosen in order to test whether the *Seismosaurus* ultrastructure is a general characteristic of long-term bone diagenesis or a more specific characteristic of either reptile bone or the bone of large land-living animals.

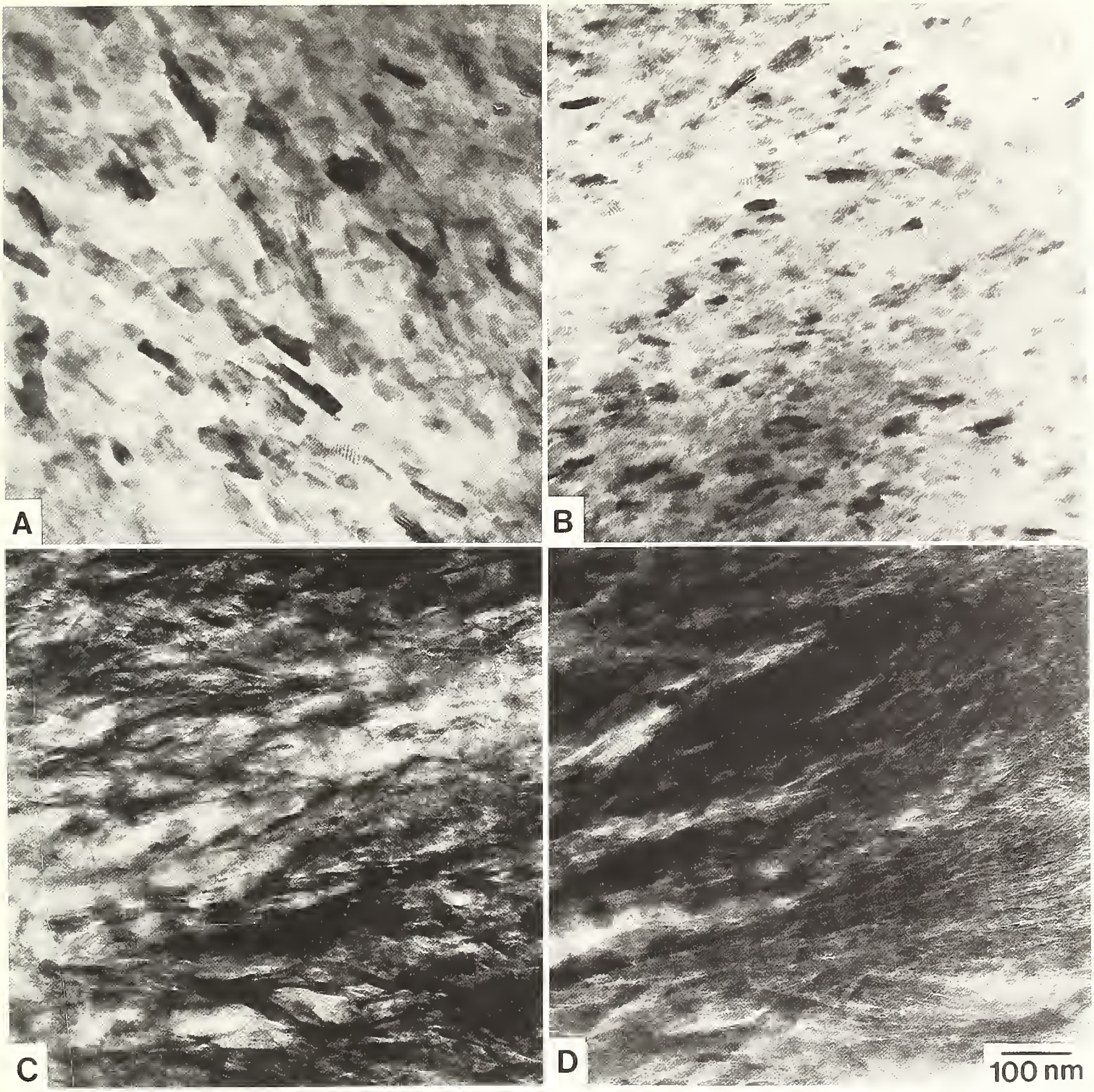
TABLE 1. List of one specimens analysed by TEM for this study.

Specimen taxon	Skeletal part	Age
Crocodile	Scute	Recent
Mammoth	Limb fragment	Late Pleistocene
Albertosaurus dinosaur	Limb fragment	Cretaceous (c. 100 Ma)
Seismosaurus dinosaur	Ischium	Jurassic (154 ± 2·4 Ma – Woldegabriel and Hagan, work in preparation)

EXPERIMENTAL PROCEDURE

Minerals such as apatite are fragile when extremely thin, and therefore, care must be taken in the preparation process to limit the amount of specimen handling. Several preparation methods were used to produce good quality TEM specimens; to produce a TEM specimen which is of any use, the thickness of the specimen in the observation area cannot exceed several hundred nanometers.

The first method involved the use of mortar and pestal to grind the bulk pieces into a fine powder which was then ultrasonically dispersed in hexane. A TEM grid coated with carbon was then dipped into the dispersion, dried, and examined in the microscope. Small pieces of bone were commonly found lying on the carbon film. These bone fragments were typically electron transparent, allowing



TEXT-FIG. 1. TEM images of representative bone apatite structure. A, *Seismosaurus*; B, theropod dinosaur; C, mammoth; D, crocodile. Note collagen fibrils in the younger bones.

both chemical and crystallographic information to be obtained, as well as direct microstructural examination.

The second method of specimen preparation preserved the natural structure of the fossilized bone and surrounding minerals by not requiring complete grinding of the bulk sample. Here the bulk sample was cut into slices which were thinned by grinding on SiC paper to a thickness of approximately 100 μm. These thin slices were then core-drilled using an ultrasonic drill with a 3 mm diameter bit. Careful handling became critical at this point, requiring vacuum tweezers to be used at all times.

Once the specimens were thinned and core-drilled, they were placed in an instrument which produced (by grinding using diamond paste) a small indent (dimple) in the specimen with a thickness of approximately 10 μm. The specimen was then ion-thinned at liquid nitrogen temperatures using argon gas at 6 kV and a 15° grazing angle until a small perforation appeared. Thinning at low temperatures helped reduce chemical migration, microstructural modifications, and knock-on damage caused by the high energy bombarding argon atoms. The dimple provided a prethinned region of the disk to minimize ion thinning time and to improve the resulting electron transparent area for TEM observation.

Examination of the specimens was performed using a JEOL 2000EX Scanning Transmission Electron Microscope equipped with a Tracor Northern Energy Dispersive Spectrometry (EDS) system. A liquid nitrogen cold stage was used to minimize electron beam damage and contamination during observation and chemical analysis.

Prepared specimens are currently stored in the Materials Division, Materials Research and Processing Science Group of Los Alamos National Laboratory, USA.

RESULTS AND DISCUSSION

Ultrastructure

TEM observation of the various bones show several distinct differences, including a variation in crystal structure between the younger and older bones, a difference in crystallite size between bones as well as within some bones, and the presence or absence of collagen fibrils. Chemical variations also existed between the bones depending on the specific intruding ionic species found in the surrounding sediment. Text-figure 1A–D shows the typical ultrastructures observed in the *Seismosaurus*, theropod dinosaur, mammoth, and crocodile, respectively. The mammoth and crocodile bones show a dense arrangement of more-or-less uniform apatite crystallites oriented parallel to a network of collagen fibrils. These crystallites are more obvious in the mammoth bone, possibly due to initial disintegration of the organic matter in the fossil.

In contrast, the *Seismosaurus* and theropod dinosaur bones show no remaining traces of collagen and include two different types of crystallites differentiated by crystal size and shape. The majority of the bone is composed of fine, oblong-shaped crystallites ranging in size from 20–30 nm wide and up to 150 nm long. Other areas contain larger crystallites which are blocky plate-shaped, and range from 50–400 nm in width and length.

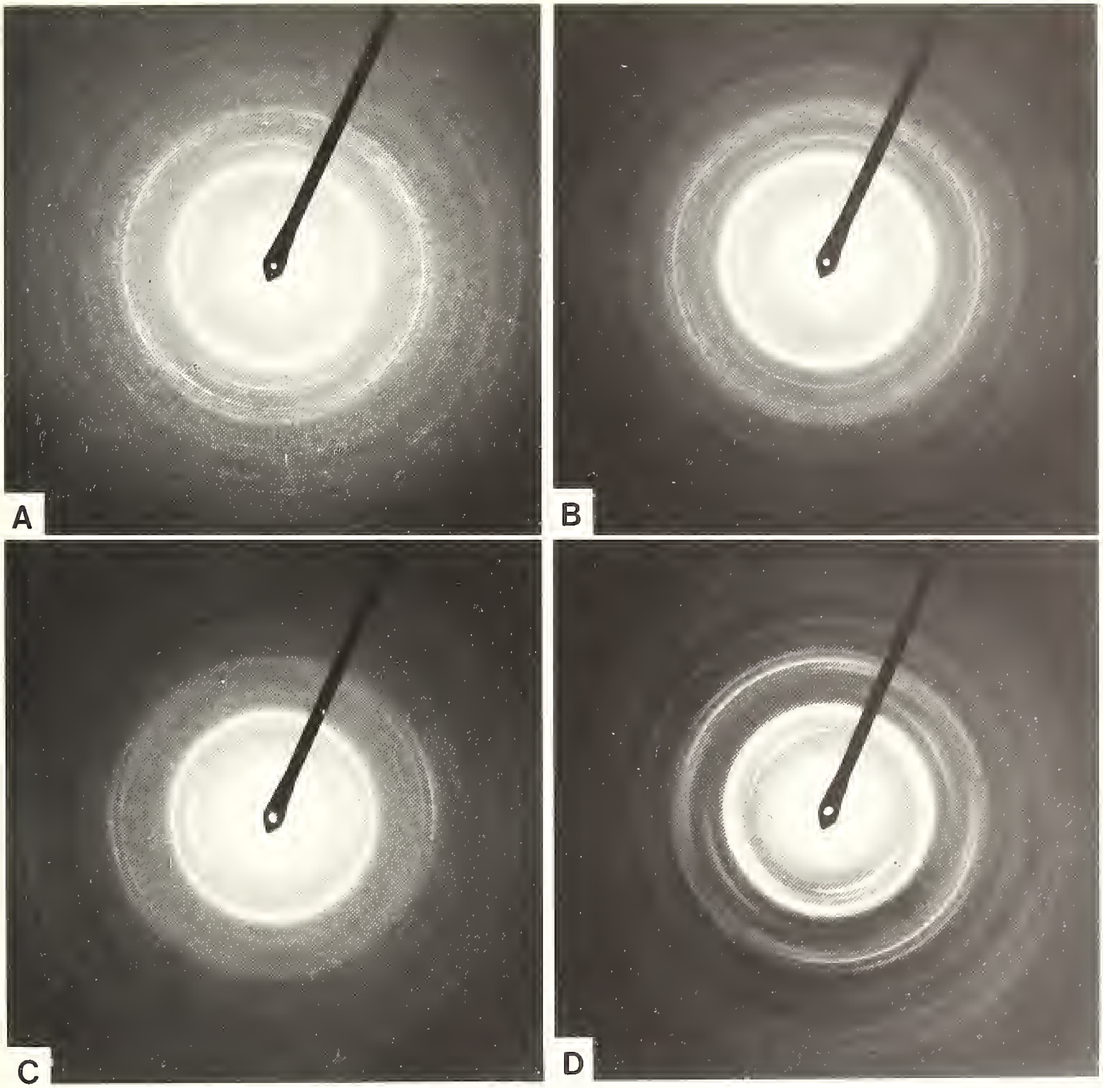
X-ray and electron diffraction

The bimodality of crystallite sizes in the dinosaur bones is easily recognized through direct observation, such as TEM or SEM imaging, X-ray diffraction (XRD) is also commonly used to measure indirectly bone crystal size, however XRD averages overall crystal size and thus cannot recognize discrete size groups easily.

X-ray diffraction of the four fossil bones studied in this investigation shows that the older bones (*Seismosaurus* and theropod dinosaur) are composed of fluorapatite, while the younger mammoth and crocodile bones are composed of hydroxyapatite.

Text-figure 2A–D shows electron diffraction patterns from fine crystalline regions (shown in Text-fig. 1), for *Seismosaurus*, the theropod dinosaur, mammoth, and crocodile, respectively. Analysis of the *Seismosaurus* and theropod diffraction patterns match what would be expected for a calcium fluoride phosphate and francolite mixture. The ratio of minerals is unknown. Electron microprobe analysis of *Seismosaurus* bone (Schwartz and Snow, work in preparation) indicates that it contains as much as 3·9 weight per cent fluorine. The patterns from the mammoth and crocodile give a reasonable fit to hydroxyapatite, as might be expected. These mineralogies are consistent with the common assumption that all fossil bone was formed originally of dahllite (carbonate hydroxyapatite), changing to francolite (carbonate fluorapatite) with time.

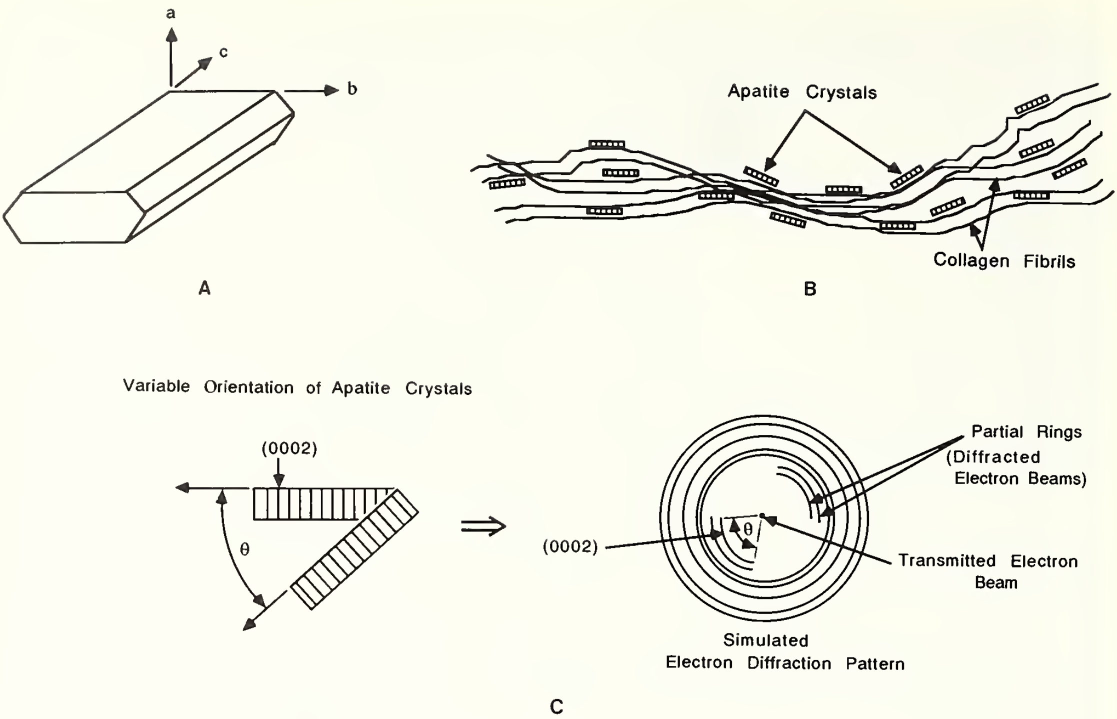
Diffuseness of the rings in the electron diffraction patterns from the younger bones may be due to the presence of a large proportion of organic material and/or to the presence of extremely fine crystallite sizes. A range of crystallite sizes is present in any one bone (Robinson and Cameron



TEXT-FIG. 2. Electron diffraction patterns taken from large clusters of apatite crystals. A, *Seismosaurus*; B, theropod dinosaur; C, mammoth; and D, crocodile bones. Partial diffraction rings indicate some degree of preferred orientation in all the fossil bones examined.

1964); the absence of the finer fraction of crystallites in fossils or sub-fossils, due to dissolution or washing out with the breakdown of organic matter (Tuross *et al.* 1989), would not be surprising.

Text-figure 3A illustrates a possible crystallographic shape of the hexagonal crystals (Cuisinier *et al.* 1987). Close examination of the crystallites present in the younger bones shows that they are oriented with their long axes parallel to the long direction of the collagen fibrils. Diffraction pattern analysis (Eddington 1976) suggests the (0001) basal planes of the hexagonal structure lie perpendicular to the length of the fibril. This is illustrated in Text-figure 3B–C, where the (0002) planes produce partial diffraction rings. Full diffraction rings indicate a random orientation. Each ring or partial ring represents a specific plane normal in the crystal structure (these are represented



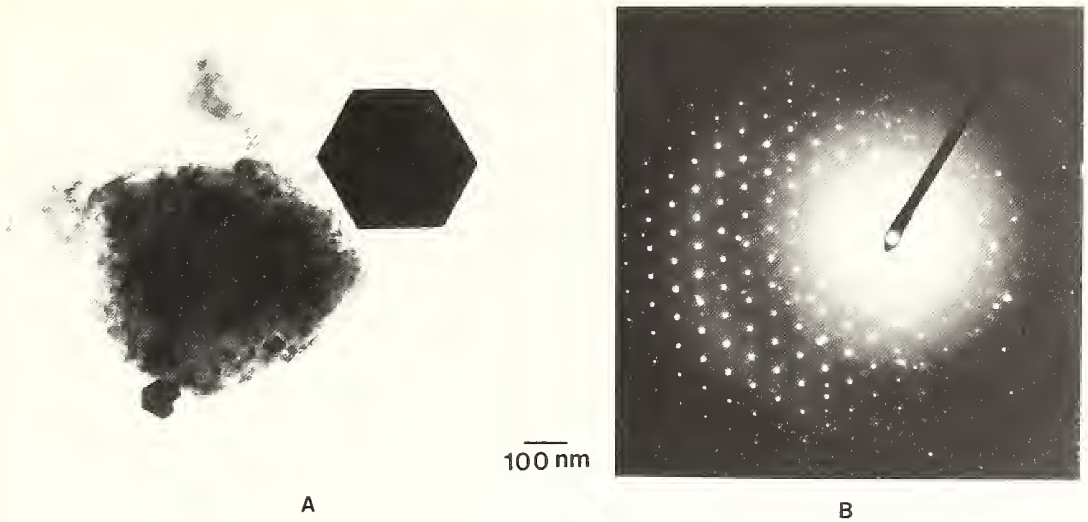
TEXT-FIG. 3. A, Schematic representation of one possible form of the hexagonal apatite crystals; both rod and plate shapes exist. B, schematic of apatite crystals lying parallel to collagen fibrils; basal planes (0001) lie perpendicular to the long axes of the crystals and collagen fibrils. C, diagram illustrating the effect of preferred orientation of apatite crystallites on the resulting electron diffraction pattern; partial diffraction rings occur with an angular relationship equal to the angular orientation range of the apatite crystals; (0002) planes are used because (0001) planes are symmetry extinct in the true diffraction pattern.

as peaks in XRD). The partial diffraction ring is produced with an arc (over the angle θ) which follows the orientation of the crystallites as they emulate the natural curvature of the collagen fibrils. This preferred orientation is also found in the older bones, indicating there may have been a similar preferred orientation apatite growth behaviour.

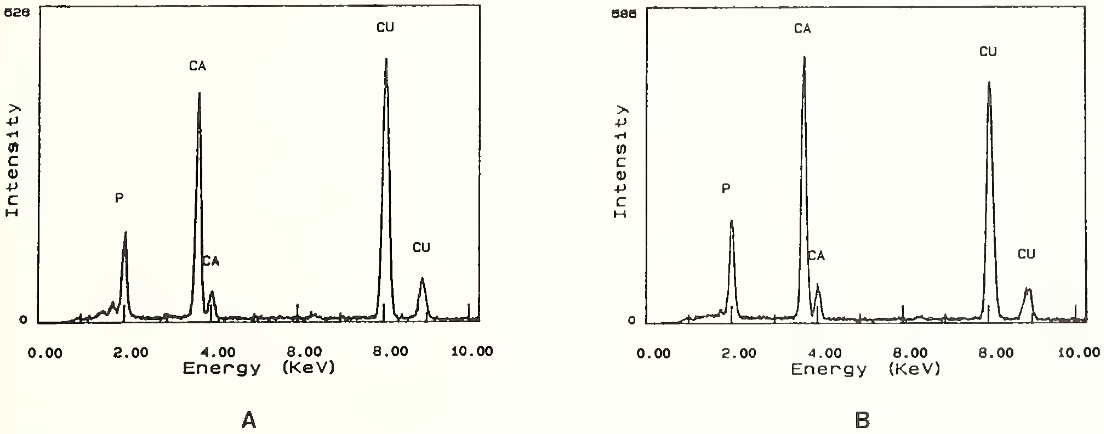
Nucleation and growth of apatite crystals

The presence of a bimodal size distribution of crystallites in the older fossils (Text-fig. 4) as compared to more recent bones shows that this peculiar ultrastructure is not a general characteristic of either reptiles or large land-living animals, and questions the similarity of bone growth in dinosaurs versus present-day animals. It is possible that dinosaur bones had unique ultrastructural features, but it seems unlikely given the relatively conservative nature of bone and skeletal evolution. A more probable scenario is that the original dinosaur ultrastructure has been modified by diagenetic processes during the millenia these bones have existed.

Electron diffraction pattern analysis (Text-fig. 2) and chemical analysis (Text-fig. 5) confirm the presence of fluorapatite crystals approximately 20 nm in length in *Seismosaurus* bone. Larger apatite crystals are also present. The larger crystallites tend to be clustered near cracks and pore spaces within the bones (Text-fig. 6). This arrangement, along with their conspicuously greater size and euhedral appearance, suggests that the larger crystallites grew under a different set of conditions

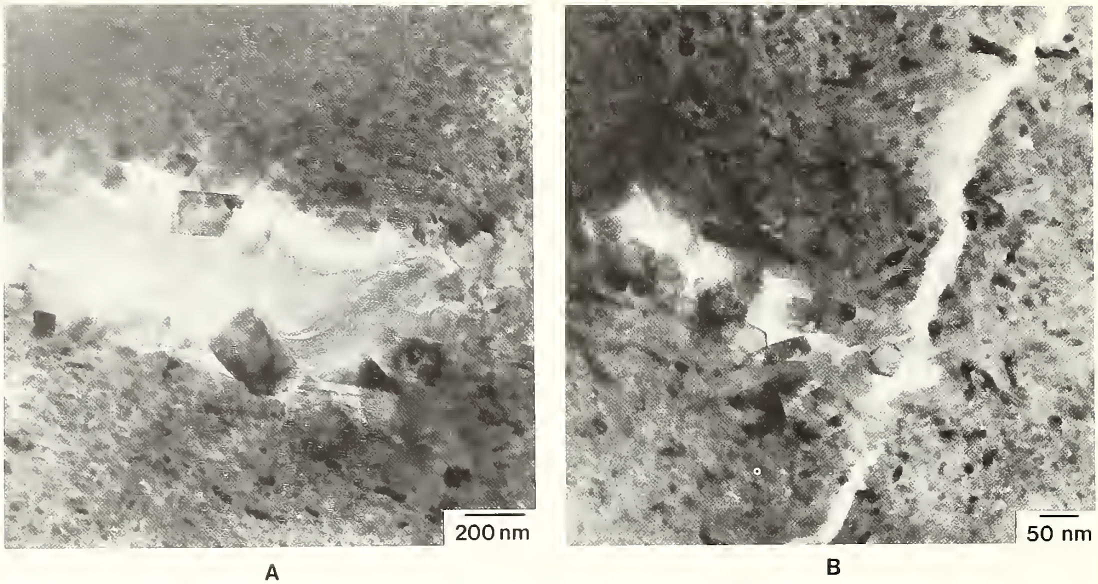


TEXT-FIG. 4. A, TEM micrograph of a region of fine apatite crystallites and a large apatite crystal exhibiting hexagonal shape (*Seismosaurus* bone). B, electron diffraction pattern of A showing the polycrystalline pattern, as well as the single crystal pattern as viewed along the c-axis, [0001].



TEXT-FIG. 5. Energy Dispersive Spectrometry (EDS) X-ray spectra taken in A, polycrystalline and B, single crystal regions found in Text-figure 4. Note copper peaks are created by the copper grid used to support the apatite crystals. Both spectra exhibit the presence of phosphorus and calcium in the crystallites in the ratio expected for apatite, (hydrogen, carbon, oxygen and fluorine are not detectable with our EDS system).

(and thus at a different time) than the smaller crystallites. It appears that they were produced by crystallization of fluorapatite from saturated liquid solution, where an aqueous medium has intruded into the bone structure. The ionic species necessary for apatite crystallization could have come either from previous dissolution of a quantity of bone mineral or from the breakdown of organic material in the bone. Both hydroxyapatite and fluorapatite are relatively insoluble (Posner *et al.* 1963), but have a range of reactivities depending on pH, temperature, and composition of the solution (Chien and Black 1975). Bone apatite solubility could also be enhanced by the large surface areas of the crystallites, the high surface reactivities of the crystallites (Posner and Betts 1975), and time.



TEXT-FIG. 6. Naturally porous regions of bones showing enhanced apatite crystal growth. A, *Seismosaurus*. B, theropod dinosaur.

Non-equilibrium conditions occurring in these bones at some time during their burial may have prompted a nucleation and growth of new fluorapatite crystals. This growth therefore resulted in larger crystals, unrelated in size to the biologically produced apatite crystals found in natural living bone. The lack of preferred orientation in the larger crystallites in *Seismosaurus* and theropod bone implies a non-epitaxial nucleation.

Previous workers have noted larger-than-normal apatite crystallites in fossil bones. Using microscopic examination, Lozinski (1973) found transparent crystals of secondary fluorapatite with a tabular habit in the haversian canals of Cretaceous dinosaur ribs. Paine (1937) petrographically identified columnar dahllite in minute cracks in a Cretaceous shark tooth.

Large, platey apatite crystallites, similar to those in our dinosaur specimens, have also been grown experimentally. Koutsoukous and Nancollas (1981) grew two different forms of hydroxyapatite crystallites at 37 °C. Most of the crystallites were needle-like, but at higher pH (7·4–8·5) with a large extent of crystal growth and in the presence of chloride, larger, plate-like crystallites formed. We believe that conditions analogous to those which produced plate-like crystals in the laboratory existed in the burial environment of the *Seismosaurus* bones (the depositional setting of the theropod remains is not known). Woldegabriel and Hagan (in preparation) showed, based on mineral assemblages, that the pH of the ancient groundwater at the site was at least 9·5. There is also evidence that fluoride (similar in size, charge and bone affinity to chloride) was abundant in that groundwater, which is confirmed by its present abundance in *Seismosaurus* bone. Finally, it is thought that the strata and fossils in the *Seismosaurus* region were subjected to burial temperatures of < 60 °C (Woldegabriel and Hagan 1990, in preparation).

CONCLUSIONS

Comparing fossil to modern bone inorganic microstructure yields unique information relating to diagenesis and palaeobiology. TEM has allowed direct visual examination of the ultra- and microstructures of *Seismosaurus*, theropod dinosaur, and mammoth bones as well as modern crocodile bone. Electron diffraction and EDS techniques were used to study the crystallography and chemistry of the apatite crystallites (francolite plus calcium fluoride phosphate). The younger mammoth and crocodile bones are composed of fine-grained hydroxyapatite crystals dispersed in a collagen fibril matrix. In all cases the apatite crystals had a local preferred orientation with the hexagonal basal planes (0001) nearly aligned, and lying perpendicular to the long axes of the collagen fibrils (when present for comparison).

The dinosaur bones are also composed largely of fine-grained hydroxyapatite crystallites, from which the finest fraction has been removed during burial and/or decomposition of the constituent organic matter within the bone. The smaller remaining crystallites are similar in size and orientation to modern bone crystallites and can be considered original. However, TEM imaging also reveals the presence of larger-sized apatite crystals, near canals and pores, in the dinosaur bones. Their random orientation and euhedral shape suggest that they are diagenetic, and formed as a result of a nucleation and growth process rather than from continued growth of existing crystallites. There is no evidence that the larger crystallites grew at the expense of the original bone material. Thus, the original microstructure of the *Seismosaurus* and theropod bones is essentially intact, only somewhat modified by the loss of the smallest fraction of crystallites and by the addition of diagenetic minerals, including apatite, to pore spaces.

Further work is necessary to confirm the process of formation of the larger apatite crystallites, to identify their distribution in other types and ages of fossil bone, and to determine what contaminating effects the presence of diagenetic apatite may have on other fossil bone analyses such as uranium and fluorine dating.

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A TERGOMYAN MOLLUSC FROM THE UPPER CAMBRIAN OF WALES

by V. BERG-MADSEN *and* J. S. PEEL

ABSTRACT. *Bellerophon cambriensis* from the Upper Cambrian of North Wales is redescribed as the type species of the new genus *Telamocornu*. Unlike most similarly coiled molluscs of this age, apertural sinuses are present which permit both a functional morphological interpretation of it as an untorted mollusc with the apex of the shall oriented anteriorly, and directly support assignation of *Telamocornu* to the Order Cyrtonellida of the Class Tergomya.

THE Cambrian was a time of innovation within the Mollusca. From examination of the fossil record, Yochelson (1963) proposed that a radiation of molluscs in the Early Cambrian was eclipsed by a second great diversification near the Cambrian–Ordovician boundary, during which most of the major mollusc groups familiar to us at the present day arose. From the point of view of anatomy, however, others have suggested that two of these late-appearing, shell-bearing groups, namely the Monoplacophora and the Polyplacophora, were ancestral stocks appearing much earlier in mollusc evolution (Salvini-Plawen 1985; Wingstrand 1985). Stimulated by models of mollusc evolution developed originally by Runnegar and Pojeta (1974), the last two decades have seen attempts to extend the range of the major extant mollusc classes back to the earliest Cambrian (Runnegar and Pojeta 1985; Yu 1990). These efforts have met with some success but a complex of mainly Early to Middle Cambrian molluscs currently lies rather uncomfortably within accepted classifications. This complex includes forms such as the Helcionelloida, elevated to a class by Peel (1991*a*, 1991*b*), the Pelagiellida, the Onychochilida and the Stenothecoida. Most of these groups were placed within an extended Class Monoplacophora alongside the well-known *Neopilina* Lemche, 1957, and its relatives (Runnegar and Pojeta 1974, 1985; Runnegar and Jell 1976), although this expansion of the concept Monoplacophora has generated discussion concerning the usefulness of the term in systematics (Wingstrand 1985; see summary in Peel 1991*b*). Thus, Peel (1991*a*, 1991*b*) followed Wingstrand (1985), Haszprunar (1988) and Salvini-Plawen (1985, 1990) and abandoned the Class Monoplacophora. He introduced a Class Tergomya for members of the *Neopilina* group (based on the Subclass Tergomya Horný, 1965). Tergomyans are oriented with the shall apex in an anterior position, while in the second major group of Lower Palaeozoic untorted and bilaterally symmetrical molluscs, the extinct Class Helcionelloida, the apex is interpreted as posterior (Peel 1991*a*, 1991*b*).

Classification of molluscs within the Cambrian is clearly in a state of flux and this instability can be expected to persist for some time as current research continues to produce startling discoveries. Not least the recent description of articulated halkieriids from the Lower Cambrian of Greenland (Conway Morris and Peel 1990) and the re-interpretation of Cambrian 'scaly-shelled' molluscs by Bengtson (1992) open a new perspective to early molluscan evolution. The abundant microsclerites and the associated larger anterior and posterior plates in the halkieriids are shell features which find morphologic equivalents in the aplacophoran and polyplacophoran molluscs which Salvini-Plawen (1985) placed in the ancestry of the later shelled forms. Moreover, halkieriids occur in strata of suitable age; aplacophorans have no fossil record and that of polyplacophorans in the Cambrian is scant.

The group of isostrophically coiled forms referred to as the bellerophontiform molluscs has a

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geological range from Cambrian to Triassic (Knight *et al.* 1960; Yochelson and Yin 1985) and has traditionally occupied a central position in discussions of the origin of the gastropods (Knight 1952; Yochelson 1967; McLean 1984; Haszprunar 1988; Horný 1991*a*). Opinions are divided as to whether members of this group were gastropods (Harper and Rollins 1982) or untorted molluscs (Runnegar and Jell 1976; Runnegar and Pojeta 1985). Peel (1991*b*) and others (Yochelson 1967; Horný 1991*a*) considered the bellerophontiform molluscs to be a mixture of both torted and untorted forms. Forms interpreted as untorted were referred by Peel to the Order Cyrtonellida of the Class Tergomya, although some genera within the Class Helcionelloida also share this coiling style (e.g. *Protowenella* Runnegar and Jell, 1976, and *Coreospira* Saito, 1936). Supposedly torted bellerophontiform molluscs were assigned to the Class Gastropoda. Unfortunately, few Cambrian bellerophontiform molluscs are readily referred to one class or the other on the basis of morphological features. Features such as an apertural slit producing a median dorsal selenizone, although previously considered to be a reliable systematic tool, are potentially developed within unrelated stocks (Rollins and Batten 1968; Yochelson 1984; Haszprunar 1988; Peel 1991*b*).

In this paper we propose a new genus of bellerophontiform mollusc from localities in the Upper Cambrian of Wales (Text-fig. 1). Unlike most contemporaneous bellerophontiform species, apertural structures are present which permit a functional morphological interpretation of this genus as an untorted mollusc, thus strengthening the record of the Class Tergomya near the Cambrian–Ordovician boundary.

SYSTEMATIC PALAEONTOLOGY

Class TERGOMYA Horný, 1965
(*nom. transl.* Peel 1991*a*, *ex* Subclass Tergomya Horný, 1965)

Order CYRTONELLIDA Horný, 1963

Genus TELAMOCORNU gen. nov.

Derivation of name. From *telamon* (Greek), belt or strap, combined with *cornu* (Latin), horn. For Thomas Belt, author of the type species.

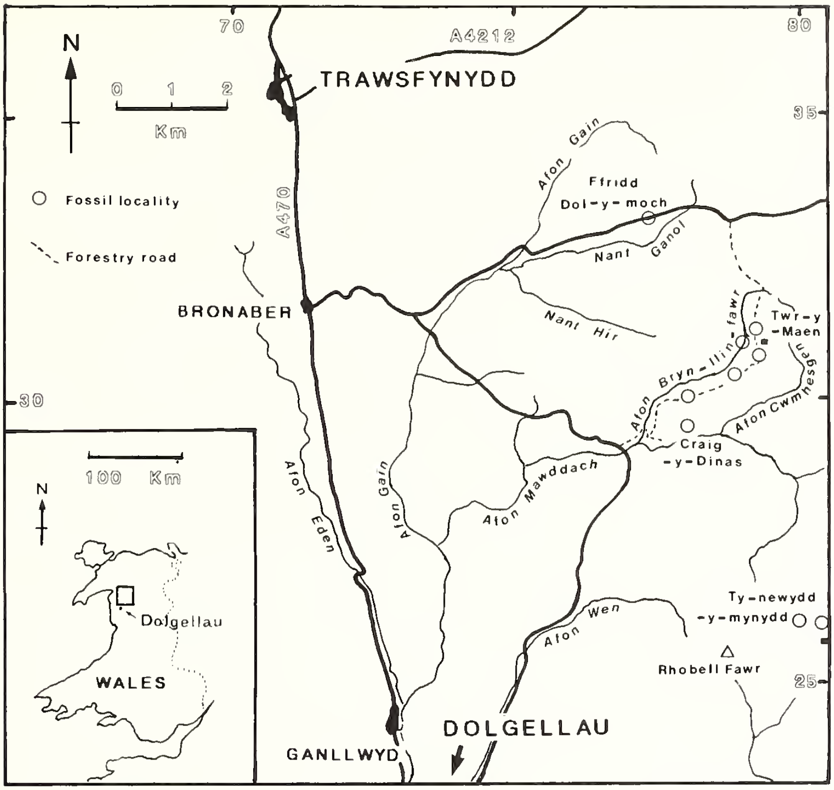
Type species. Bellerophon cambriensis Belt, 1868.

Diagnosis. Loosely coiled, in early stages open coiled, rapidly expanding but laterally compressed cyrtonellid tergomyan with about 1·5 whorls. Dorsum uniformly convex; aperture with broad and shallow median sinus and tendency to produce umbilical sinuses. Ornamentation of transverse rugae and fine growth lines, crossed by weak spiral lines.

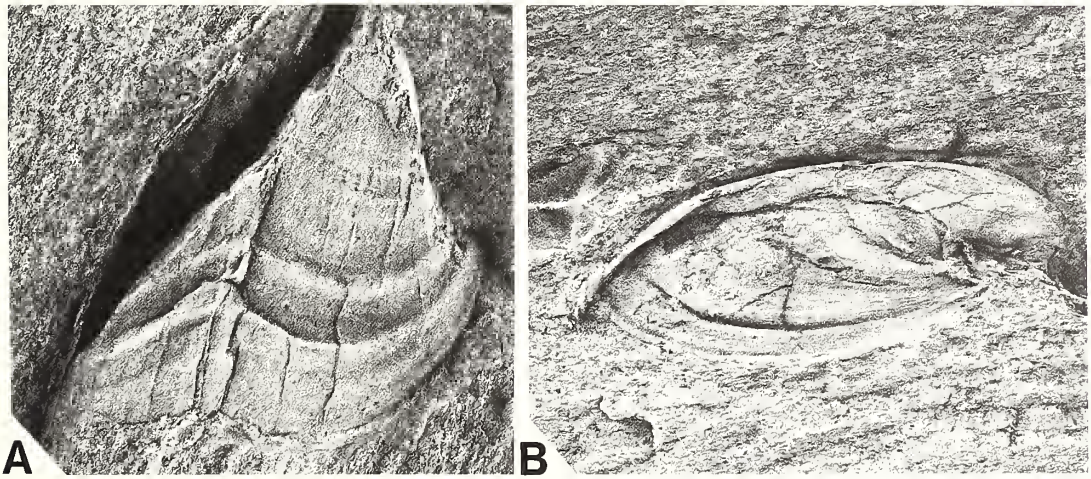
Discussion. Most of our knowledge of Late Cambrian bellerophontiform molluscs stems from two papers (Knight 1947, 1948) mainly based on North American material. In these papers, six new genera were described (*Anconochilus*, *Chalarostrepsis*, *Cloudia*, *Cycloholcus*, *Sinuella* and *Strepsodiscus*) and *Owenella* Ulrich and Scofield, 1897 redescribed. He also redescribed *Coreospira* Saito, 1936, from the Middle Cambrian of Korea and British Columbia but this genus, and possibly also *Cycloholcus*, is an unusual helcionelloid.

Of the genera listed above, only *Anconochilus* from the middle Upper Cambrian (Franconian) can be closely compared to *Telamocornu* of similar age; it is distinguished by being more involute and less rapidly expanding. Ornamentation is poorly known in *Anconochilus barnesi* Knight, 1947, the type and only described species, but Knight (1947) recorded a shallow median sinus in the apertural margin.

Telamocornu closely resembles *Sinuitella* Yochelson, 1962, from the Lower Ordovician (Tremadoc) of Norway. It is distinguished, however, by its much larger size (*c.* 22 mm compared with 5–8 mm for *Sinuitella norvegica* (Brogger, 1882) and greater rate of whorl expansion, particularly antero-posteriorly. *Sinuitella norvegica* is open coiled, with the whorls not in contact,



TEXT-FIG. 1. Localities of Cambrian tergomyan molluscs described in the text (modified from Allen *et al.* 1981).



TEXT-FIG. 2. *Telamocornu cambriense* (Belt, 1868). Upper Ffestiniog Flags Formation; ×3; BM62087. A, lectotype; fragment of dorsal surface showing transverse rugae and median sinus. B, paralectotype; lateral view of specimen crushed in shale.

whereas *Telamocornu* is apparently loosely coiled in larger specimens, with shallow impression of the earlier whorl.

Pharetrolites Wenz, 1943 is similar in general form to *Telamocornu* but has a lower rate of whorl expansion. This Silurian genus is also distinguished by its deeper median dorsal sinus and crenulate ornamentation.

Latouchella aperta Orlowski, 1968 from the Upper Cambrian of the Holy Cross Mountains of Poland is more tightly coiled than *Telamocornu cambriense* and seems to have a more angular dorsal profile; Orlowski's original generic assignment is highly questionable.

Jago and Corbett (1990, fig. 2F–J) figured three bellerophontiform molluscs from a topmost Cambrian sandstone-siltstone sequence in western Tasmania. Their 'Bellerophontida gen. et sp. indet. 1' resembles *Telamocornu* in its rate of expansion and size, whereas two other indeterminate forms are more laterally compressed, with an arched dorsal profile.

Telamocornu cambriense (Belt, 1868)

Plate 1; Text-figure 2

1868 *Bellerophon Cambriensis* Belt, p. 11, pl. 2, figs 19–20.

Type material. Lectotype (here designated) is the specimen figured by Belt (1868, pl. 2, fig. 20); paralectotype, the original of Belt (1868, pl. 2, fig. 19). Both specimens (Text-fig. 2) carry the registration number BM 62087, and were collected at Craig-y-Dinas, Dolgellau district, North Wales, in strata containing *Parabolinoides bucephalus*, indicative of the uppermost part of the late Cambrian Ffestiniog Flags Formation.

Other material. A collection (BGS Zv9778, Zv9781, Zv9783–86, Zv9788, Zv9789) made by Stephen Jusypiw and presented to the British Geological Survey, comes from a fine-grained sandstone occurring at about the same horizon as the types on the Bryn-llin-fawr forestry road (National Grid Reference SH 7865 3035); the fauna (Pl. 1, figs 4–10) is assigned to the Zone of *Parabolina spinulosa.* Poorly preserved specimens (BGS RU9708A–B, collected by A. W. A. Rushton), possibly assigned to *Telamocornu* also occur in the underlying Maentwrog Formation (*cataractes* Subzone of the *Olenus* Zone) at Ffridd Dol-y-Moch on the Llanuwchllyn road, 7 km ESE of Traswfynydd (SH 7648 3298; Allen *et al.* 1981, p. 308), and in the Dolgellau Member (*Acerocare* Zone) of the Cwmhesgen Formation (BGS RU5281, collected by A. W. A. Rushton and S. P. Tunnicliff) which overlies the Ffestiniog Flags Formation (Ty-newydd-y-mynydd, 1·5 km E of Rhobell Fawr; Allen *et al.* 1981, p. 317 (SH 7996 2601), cf. Rushton, 1982, Text-fig. 1). In terms of the North American standard, these occurrences range from the upper Dresbachian (Upper Cambrian) upwards to the Cambrian–Ordovician boundary.

Description. (Based on two suites of specimens (see above), since the types are imperfectly preserved.) Type species of *Telamocornu* gen. nov. with about 1·5 whorls. Earliest growth stage apparently consisting of the rather blunt origin of the coil, not distinguished in terms of coiling or ornamentation from subsequent growth stages; the umbilici were probably perforate. In the latest preserved growth stage the whorls appear to be loosely in contact and the shell is laterally compressed, with width about half of the total length. The dorsum

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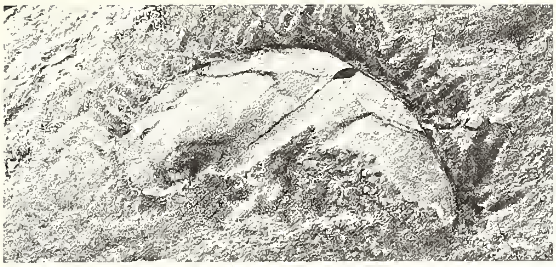
EXPLANATION OF PLATE 1

Figs 1–3. *Telamocornu cambriense* (Belt, 1868)? Poorly preserved specimens in lateral view. 1, BGS RU9708A; Maentwrog Formation; ×3. 2, BGS RU9708B; Maentwrog Formation; ×3. 3, BGS RU5281; Cwmhesgen Formation; showing fine transverse and spiral ornamentation; ×2.

Figs 4–10. *Telamocornu cambriense* (Belt, 1868). Ffestiniog Flags Formation. 4, BGS Zv9788; lateral view to show the external mould of the early growth stages; ×1·5. 5, same specimen in oblique dorsal view to show the convex dorsum; ×1·5. 6–7, BGS Zv9789; latex mould and corresponding external mould showing the umbilico-lateral sinus interpreted as inhalant in function; ×8. 8–10, BGS Zv9785; two specimens preserved as internal moulds with early growth stages broken away. 8, lowermost of two specimens figured in 9 (×4) showing external mould of earliest growth stages and internal mould of apertural region with transverse rugae; ×8; 10, dorsal view of upper specimen showing rounded dorsum; ×4.

PLATE 1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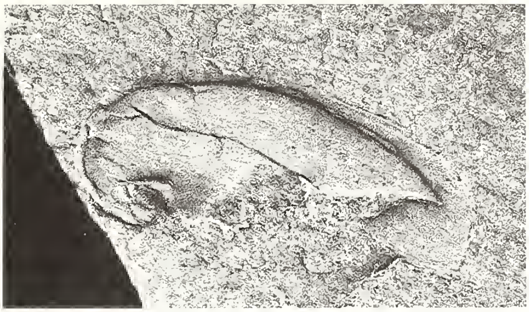
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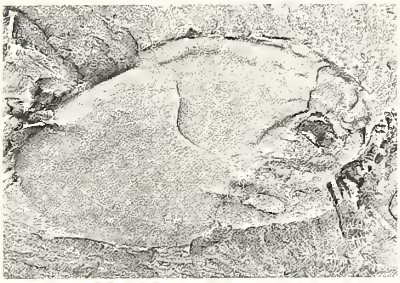
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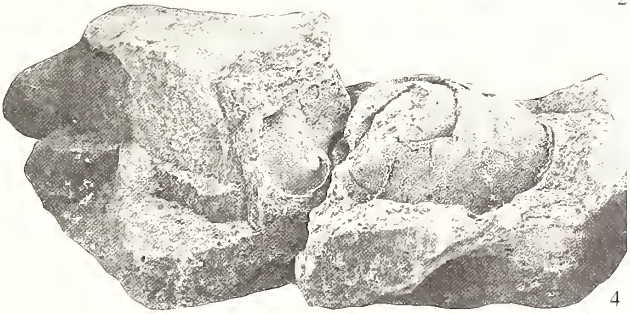
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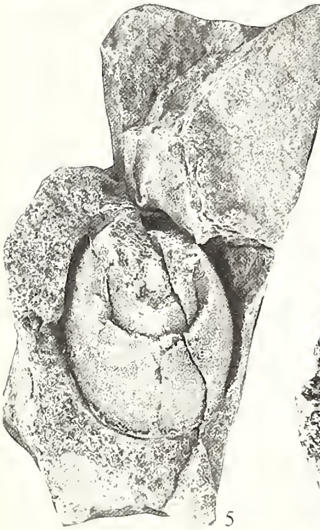
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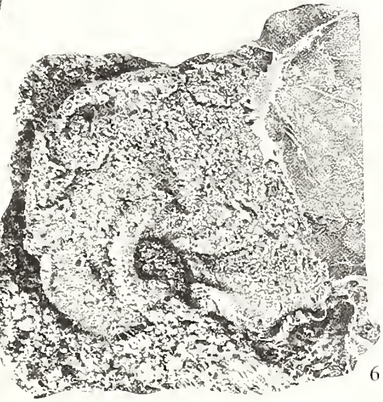
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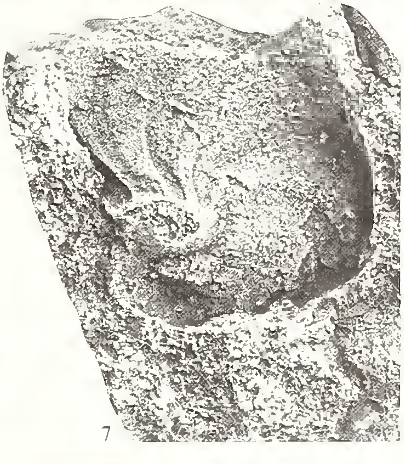
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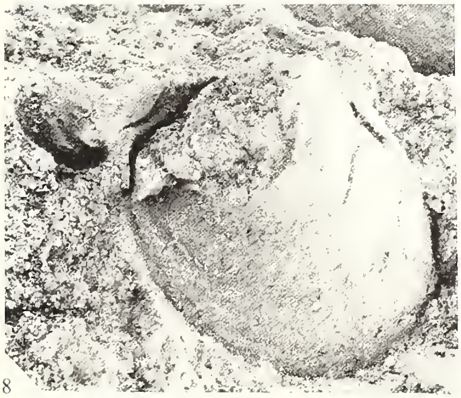
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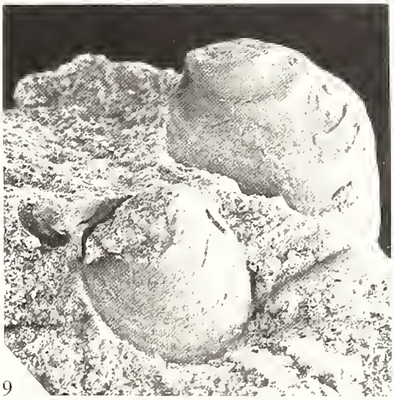
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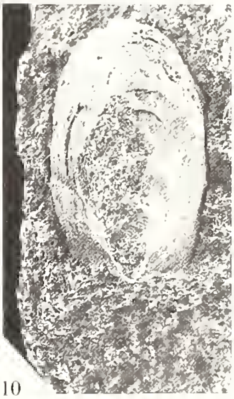
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BERG-MADSEN and PEEL, *Telamocornu*

is convex, uniformly rounded, without median angulation or a keel. In plan view, the length:width ratio of the aperture is about 3:2. The aperture is sinuate having a broad, shallow, emargination in the mid-dorsal margin; apertural margins appear to be essentially co-planar but in laterally crushed specimens the lateral areas are adaperturally convex. A tendency for small sinuses to develop on the umbilico-lateral surface, near the suture with the previous whorl, is observed in a few specimens.

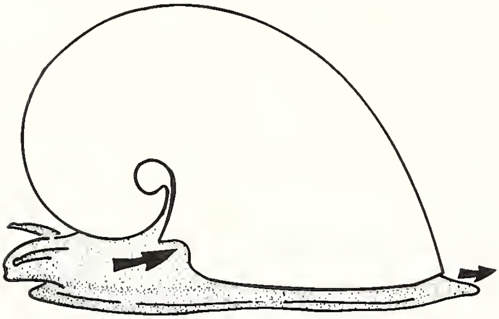
Ornamentation consists of transverse growth rugae, apparently produced by periodic slight expansion of the dorsal apertural margin, and fine growth lines, crossed by weakly developed, fine spiral lines. Shell thickness and structure are unknown.

Only a portion of the dorsal surface is preserved in the lectotype but this clearly shows the median dorsal sinus; the apparent median band is a result of crushing. The paralectotype is crushed in lateral view and also shows an apparent keel due to fracture along the periphery; the adaperturally convex curvature of the lateral margins is exaggerated by crushing.

The largest of the specimens from Bryn-llin-fawr (Zv9788; Pl. 1, figs 4–5) shows the early growth stages as an external mould of the lateral surface, while the partially embedded aperture is preserved as an internal mould. Notable among specimens from this locality is one (Zv9789) preserved as an external mould of the lateral surface, showing a sinus on the umbilico-lateral margin (Pl. 1, figs 6–7) which is interpreted below as having served an inhalant function.

FUNCTIONAL MORPHOLOGY OF *TELAMOCORNU*

Few of the genera and species of bellerophontiform molluscs currently known from the Upper Cambrian and Lower Ordovician preserve morphological features of the shell which facilitate interpretation of their systematic affinities either with the Gastropoda or with the Tergomya (the presence of some helcionelloid taxa within this plexus also cannot be excluded). An important feature in such interpretations is the presence and distribution of emarginations in the apertural margin. *Sinuitella*, as illustrated by Yochelson (1962, pl. 1, fig. 7), preserves a shallow sinus at the umbilico-lateral shoulder reminiscent of those noted above in *Telamocornu cambriense* (Pl. 1, figs 6–7; Text-fig. 3). Horný (1991*b*) described similar structures in *Sinuitopsis neglecta* Perner, 1903 from the Ordovician of Bohemia. Such sinuses are also described in specimens of younger age, such as *Pharetrolites bambachi* Peel, 1975 from the Silurian Arisaig Group of Nova Scotia (Peel 1975).



TEXT-FIG. 3. Reconstruction of *Telamocornu cambriense* (Belt, 1868) as a tergomyan mollusc, with the anterior to the left. Water currents (arrows) enter the mantle cavity anteriorly, by way of the umbilico-lateral sinus (cf. Pl. 1, figs 6–7) located on each side of the shell, prior to exhalation via the posterior median dorsal sinus.

The umbilico-lateral sinuses can be interpreted as the locus of inhalant currents entering the mantle cavity, with the median dorsal sinus marking the position of the posterior exhalant stream (Text-fig. 3). If the exhalant stream is posterior, the shell is coiled exogastrically, with the initial whorls located anteriorly, overhanging the anterior margin of the aperture (Peel 1991*b*, p. 19, fig. 12). Following this reconstruction, *Telamocornu* (together with *Sinuitella*, *Sinuitopsis* and *Pharetrolites*) is interpreted as an untorted, exogastric, bilaterally symmetrical mollusc, a cyrtonellid tergomyan in the sense of Peel (1991*b*). If *Telamocornu* is interpreted as torted, and assigned to the Gastropoda, the shell would be endogastric with the earlier coiled portion located posteriorly. This interpretation, however, is not supported by the presence of the supposed inhalant umbilico-lateral sinuses.

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CARBONIFEROUS ORTHOSTERNI AND THEIR RELATIONSHIP TO LIVING SCORPIONS

by ANDREW J. JERAM

ABSTRACT. Five species of Upper Carboniferous orthostern scorpions are described from Britain and North America. Two are established taxa, and three are new: *Palaeopisthacanthus vogelandurdeni* sp. nov., *Cryptoscorpius americanus* gen. et sp. nov., and *Corniops mapesii* gen. et sp. nov. An additional species, *Gymnoscorpius mutillidigitus* gen. et sp. nov., is referred to the suborder Neoscorpionina, but is too incompletely known for its systematic position to be determined more accurately. The descriptions are based on fragmentary material from dispersed arthropod cuticle assemblages. These have yielded sufficient anatomical detail to assess the relationship between fossil and Recent orthostern scorpions for the first time. A cladogram is presented, demonstrating that Carboniferous orthosterns comprise the stem group from which all Recent scorpions (the crown group) were derived. The recognition of important character state transition series in the Orthosterni, and their polarities, will facilitate more accurate assessment of the relationships between modern scorpion genera.

THE fossil record of scorpions has been largely ignored by neontologists in discussions about the origins of modern scorpion families and the relationships between them. This is understandable, as the quantity of fossil data having a bearing on these problems is small, and its quality poor. Most fossil scorpions are Palaeozoic forms, and the handful of described Mesozoic species are essentially Palaeozoic relics. By contrast, all reasonably well preserved Cenozoic fossil scorpions are thoroughly modern in aspect and can be assigned to extant families, if not genera (e.g. Schawaller 1979, 1981).

Among fossil families, only the Palaeopisthacanthidae span the gulf between the diverse Palaeozoic record of scorpions and the Cenozoic to Recent fauna. Kjellesvig-Waering (1986) included two Upper Carboniferous species in this family, *Palaeopisthacanthus schucherti* Petrunkevitch, 1913, and *Compsoscorpius elegans* Petrunkevitch, 1949. One specimen of the former species, and three of the latter, were available to Kjellesvig-Waering. These are reasonably well preserved in ironstone nodules, but even so, most anatomical details which are of importance in the classification of Recent scorpions cannot be ascertained, and Stockwell (1989) concluded that these species are so 'modern' in their gross morphology that if more characters were available, they could probably be placed within Recent superfamilies.

A systematic search for dispersed scorpion cuticle fragments in Carboniferous sediments has yielded exceptionally well preserved material which reveals morphological detail unobtainable from typical scorpion body-fossils (Bartram *et al.* 1987). During the course of this study in excess of 20000 cuticles (a conservative estimate) from twenty two Carboniferous localities have been examined. The material is largely fragmentary, consisting of cuticle scraps (around 80% of most asemblages), isolated exoskeletal elements, and very rarely, associated body parts from a single individual. Palaeopisthacanthid cuticle forms only a small proportion of each scorpion cuticle assemblage, but even tiny fragments are easily recognizable because they have a distinctive surface ornament. This paper describes all of the palaeopisthacanthid material recovered to date, and two additional forms which have closer affinities to the palaeopisthacanthids than to any other Carboniferous family.

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LOCALITIES AND MATERIAL

Localities

Details of localities from which the palaeopisthacanthid type of cuticle has been obtained are listed below in stratigraphical order. The productive lithologies are either coals or carbonaceous shales rich in comminuted plant debris, and all appear to have been deposited in forested flood-basin environments.

1. Goyt's Clough, near Buxton, Derbyshire, England; NGR SK 0272. Shaly coal from the top 0·3 m of Goyt's Coal; basal Westphalian A.
2. Glodwick Brickworks, Oldham, Lancashire, England; NGR SD 9404. Bituminous coal from the Blenfire Seam; high Westphalian A.
3. Coby Carr Quarry, near Todhills, Co. Durham, England. Bituminous coal from the Bottom Busty Seam; high Westphalian A.
4. Pemberton Opencast Mine, Near Wigan, Lancashire, England. Carbonaceous shale from a seam split in the Wigan Five Foot Coal; uppermost Westphalian A.
5. Swillington Brickpit, Swillington, Yorkshire, England; NGR SE 385315. Carbonaceous shales occurring as seam splits and roof shales in sequences of thin coals at three horizons (beds 13, 18, and 20F of Scott (1978, 1984)); low Westphalian B.

6*a*. Lowther North Opencast Mine, near Leeds, Yorkshire, England; NGR SE 403282. Bituminous coal from the Barnsley Seam; low Westphalian B.

6*b*. Wistow Mine, Yorkshire, England; NGR SE 5936. Bituminous coal from the Barnsley Seam; low Westphalian B.

7. United Electric Companies Banner Mine, Foulton County, Illinois, USA; SE1/4, NW1/4, Sec. 12, T, 6N, R. R. 5E. Bituminous coal from the Colchester (no. 2) Coal, Carbondale Formation; Westphalian D (Desmoinensian).
8. Lone Star Lake Spillway, Douglas County, Kansas, USA; NW 1/4, Sec. 13, T. 145., R. 18E. Carbonaceous shale from immediately above the Lower Williamsburg Coal, Douglas Shale Formation; Stephanian B (Virgilian). See Landingham (1961) for further details of the locality.

Material

All cuticle material used in this study is deposited at the Ulster Museum, Belfast (BELUM). For brevity the Ulster Museum code (BELUM) has been omitted when referring to cuticle specimens in the text or figure legends, which are all prefixed by 'K'. Body fossils referred to in the text are located at the Natural History Museum, London (BMNH), and Yale Peabody Museum (YPM). The Appendix lists all significant cuticle specimens used in this study, but unidentifiable sclerites and cuticle scraps derived from palaeopisthacanthids are not listed.

METHODS

Standard palaeobotanical techniques were employed for the extraction of dispersed arthropod cuticles from sediment bulk samples (e.g. Funkhover and Evitt 1959; Staplin *et al.* 1960). Coals were macerated in fuming nitric acid, but exposure to acid for more than two to three hours resulted in some corrosion of scorpion cuticles, and exposure for over one day destroyed them. It is possible that this treatment removes cuticles of some arthropod groups which are less acid resistant, but there was no way to check this. Dark carbon-rich shales were disaggregated efficiently in 100 volume hydrogen peroxide, whilst soft shales were soaked in dilute potassium hydroxide solution for several days.

Residues were wet sieved, and typically consist of a mass of plant cuticles, palynomorphs, carbonized plant material and occasional arthropod cuticles. The smallest useful fraction was retained on a 250 μm aperture sieve. Finer residue fractions were routinely checked for the presence of microarthropod remains. Residues were examined under water by transmitted light, which enables arthropod cuticles to be picked readily from among plant debris. Cuticles were stored in two percent hydrochloric acid, since those stored in water are readily susceptible to fungal and bacterial attack.

Before mounting on microscope slides, material from shales generally required cleaning to remove adherent clay minerals which obscure detail in transmitted light. Most clay can be removed mechanically with a fine needle, but the best results were obtained by soaking batches of cuticle in sixty percent hydrofluoric acid for several hours. Organic material, much of it opaque, is often so firmly bonded to the cuticle that it is difficult to remove without damaging the specimen.

Many specimens were folded on themselves prior to burial (see below), but in some cases these can be unfolded by careful manipulation in the mounting medium before the cover slip is positioned. The study of flattened cylindrical sclerites, such as postabdominal segments, is facilitated by slitting the cuticle along one margin. The opposed layers of cuticle can then be separated and mounted as a single sheet rather than two surfaces compressed together.

Specimens were mounted on glass microscope slides in glycerol jelly, Aquamount, or Aqualite. Transmitted light microscopy proved to be the most useful means of study, employing an Olympus SZH Stereo Zoom Microscope, and a Nikon Optiphot biological microscope fitted with a Normaski Differential Interference Contrast (NDIC) facility.

Specimens are oriented in the illustrations with anterior ends towards the page top, with the exception of prosomal appendage sclerites, which are oriented with the superior surface towards the page top and distal end to the right, unless otherwise indicated in the legend. Explanatory figures were prepared from *camera lucida* drawings made on the Olympus SZH microscope. Stippled areas are internal cuticle surfaces and dotted lines represent linear features showing through the cuticle from behind. In specimens with overlapping layers of cuticle, e.g. podomeres, cuticular features such as follicles, spines and tubercles on all layers are shown, not only the uppermost. Artifacts, plant debris and opaque organic matter have been omitted from most text-figures. Abbreviations used in text-figures are as follows: St, sternite; T, tergite; Co, coxa; Ca, coxal apophysis; S, sternum; Cp, carapace; Go, genital opercula; tf, anterior transverse ridge; sm, stigma; ic, inferior carina; sc, superior carina; im, inferior median carina; il, inferior lateral carina; sl, superior lateral carina; dc, dorsal carina; ss, secondary tubercular structure; b, basal tooth; m, median tooth; sd, subdistal tooth; d, distal tooth; i, inferior row of teeth; a, ?arachnid podomeres; mi, mite remains; ts, tibial spur; dt, dorsal tubercle; le, lateral eye node; me, median eye; fe, femur; tr, trochanter; D, opaque detritus.

Trichobothrial terminology and abbreviations used are those of Vachon (1973), whilst podomere terminology follows that of Couzijn (1977), and other scorpion terms are those recommended by Stahnke (1970).

PRESERVATION AND TAPHONOMY

Preservation

The material is preserved as thin sheets of organic cuticle (Bartram *et al.* 1987). The sheets are flexible when wet, but become brittle on drying. Average cuticle thickness is 2–4 μm, the thinnest cuticles being almost colourless, with thicker ones (from larger individuals) grading from pale yellow through to orange-brown. Most specimens recovered are small scraps of cuticle consisting of a single sheet. Fragmentary material which can be recognized as a particular sclerite type is scarce, and complete sclerites or associated groups of sclerites (i.e. partial individuals) are rare. All material is compressed, leading to complex collapse folding of the originally three dimensional structures. In other respects the cuticle preservation is similar to that described by Selden *et al.* (1987) for Devonian arachnid cuticle compressions. Scanning electron microscopy (SEM) of thick cuticles from very large Carboniferous (non-orthostern) scorpions has revealed that only an outer region of the cuticle equivalent to the hyaline exocuticle of Recent scorpions is preserved. The thinness of preserved cuticle, in relation to the original body length of these scorpions, suggests that this is also the case for the orthostern cuticle described below.

Taphonomy

Dispersed scorpion cuticles are invariably preserved in association with fragmentary plant cuticles and palynomorphs. They are most frequently encountered in horizons rich in comminuted plant debris, such as the roof shales of coal seams and shaly partings (splits) within seams. The great majority of cuticles are derived from immature individuals, but occasional larger specimens indicate the minimum adult sizes reached by each taxon. The cuticle could be derived from moulted exoskeletons or dead animals. There is little direct evidence for the latter, apart from some rare aggregates of finely comminuted cuticle which may be arachnid rejectamenta, or possibly the remains of cuticle rich coprolites. Evidence for moulted integuments is more frequent, and includes 'telescoped' abdominal regions, and distal podomeres which were pulled inside proximal ones as the leg was extricated from the exuvium.

Maceration residues contain a range of material with different degrees of fragmentation, which on the basis of sclerite sizes must have come from many different individuals. Most disarticulation and comminution, therefore, occurred prior to burial, although the occurrence in a residue of fragments which can be fitted together suggests that some fragmentation of sclerites, but not individuals, was due to diagenetic compaction of the cuticle and/or the cuticle recovery process.

A variable proportion of cuticles in each assemblage show evidence of partial degradation by saprotrophic microorganisms. Corrosion of the outermost preserved layer of cuticle is common, and SEM examination of corroded surfaces reveals clusters of small pits which may be attributable to the former presence of bacterial plaques. More convincing evidence is provided by star-shaped scars with anastomosing branches, identical to those attributed to actinomycetes in palynomorphs (Elsik 1971). No remains of the saprotrophs responsible were found *in situ*, ruling out the possibility that the degradation is due to recent contamination.

A few cylindrical sclerites contain the remains of mites, or other arthropods, compressed between the two layers of cuticle. Mites may have entered the disarticulated sclerites to feed, or perhaps used them as moulting refugia, but in either case owe their preservation to this habit since, with the exception of the Lone Star Lake assemblage, articulated mite remains do not occur free in the cuticle assemblages examined.

The cuticle assemblages probably represent detrital arthropod material accumulated in a leaf litter layer. Residence times of cuticle in the litter were variable as evidenced by the different degrees of comminution and degradation shown by cuticles in an assemblage. Rapid establishment of post-burial anoxic conditions may have been a prerequisite for preservation because scorpion cuticle, including the hyaline exocuticle, is rapidly degraded in aerobic conditions (pers. obs.; but see Allison and Briggs 1991 on the role of anoxia on soft-bodied fossil preservation). Since non-hyaline procuticle (inner exocuticle and endocuticle) is not present in the fossil material, the decomposition of these layers probably continued after burial in an anoxic environment. An abundance of plant material buried in association with the scorpions may have been a significant factor in the reduction of available oxygen in the sediment. Why anaerobic saprotrophs did not continue degrading the scorpion cuticle (and indeed the plant cuticle) after burial is unknown.

No remains of uniramians were found in any assemblage, and cuticle of other arachnids only occurred in assemblages where scorpion cuticles display very low average degrees of degradation. The scorpion hyaline exocuticle layer is apparently unique to scorpions (Hjelle 1990), but an analogous layer may also occur in xiphosurans and eurypterids (Dalingwater 1986). Scorpion hyaline exocuticle (or its equivalent in Palaeozoic scorpions) appears to be far more resistant to anaerobic decay than the cuticle of other arthropods.

DISPERSED CUTICLE TAXONOMY

The difficulties involved in dispersed cuticle taxonomy were discussed by Wills (1947). His work on a Triassic cuticle assemblage is the only previous study which has attempted to deal with dispersed material, and his methods are adopted here, with some modifications. More recently, a Middle Devonian arthropod cuticle assemblage, the Gilboa fauna, has underlined the value of such material, radically altering our perception of early terrestrial faunas (Shear 1990). However, until now, taxonomic work on the Gilboa fauna has relied heavily on the rare occurrence in that assemblage of relatively complete specimens to which the more fragmentary remains add supplementary data (Shear *et al.* 1987; Selden *et al.* 1991).

The Upper Carboniferous assemblages from which the palaeopisthacanthid material described here was obtained were initially sorted into scorpion and non-scorpion cuticles. The scorpion cuticle was further sorted according to characteristics of the cuticle surface texture, the style and distribution of ornament, setation, colour, and refractivity (brightness) of the cuticle.

Palaeopisthacanthid-like cuticle was then sorted according to sclerite type, and these groups carefully studied to determine how many forms of each sclerite type are present. At this stage morphological differences due to intraspecific variation, ontogeny, sexual dimorphism, and taphonomic effects, may all be present. For reasons of parsimony, it is assumed that only one species is present at each locality, unless differences exist between sclerites which cannot be attributed to any of the factors responsible for variation cited above.

The Lone Star Lake assemblage, for example, contains three forms of pedipalp chelae, which for reasons discussed below are each believed to represent a separate species. Although differences do exist between specimens in other sclerite groups (e.g. femora, Pl. 5, figs 7, 9–10), they include characters such as cuticle thickness, the relative proportions of sclerites, and surface ornament distribution, which are all likely to vary intraspecifically, from somite to somite on a single individual, through ontogenic development, and also due to sexual dimorphism. It was therefore not possible with the limited amount of material available to sub-divide the sclerite groups reliably, and for this reason all other specimens in the assemblage are provisionally assigned to the most common species (one chela form is presented by 11 specimens, the other two are based on single specimens). In the English Upper Carboniferous assemblages, no good grounds were found for sub-dividing any of the sclerite groups, so all material in each assemblage is attributed to a single species.

Once the minimum possible number of species represented in an assemblage has been determined and the general characteristics of those species identified, each assemblage was compared with the others to establish if one species was present in more than one assemblage. Finally, the collection as a whole was compared with available body fossils to try and identify any previously described forms. This procedure conforms with the recommendations made by Bengtson (1985) for sclerite-based taxonomy.

COMPARISON WITH BODY FOSSILS

Scorpion body-fossils are frequently well preserved compared with those of other terrestrial arthropods, but nevertheless taphononic effects can make the remains very difficult to interpret. Characters employed in the taxonomy and systematics of fossil scorpions have tended to be those relating to gross body form, such as the structure of the coxosternal region, carapace shape, abdominal plate structure and the relative proportions of various body parts. Although the dispersed cuticle material is very well preserved, its fragmentary nature means that many of these taxonomically useful characters cannot be determined. Comparisons between body fossils and dispersed cuticles are therefore not easily made.

It is, however, possible to build up a set of characters observed in fragmentary material from an assemblage which can be used as a basis for comparisons. For the material under consideration, these are as follows:

1. The largest specimens, presumably from adults, come from scorpions with an estimated length of < 50 mm. This is unusually small for adult Carboniferous scorpions, several of which reached 300 mm in length.
2. All of the sternite fragments recovered have round intrasternite stigmata.
3. Trichobothrial follicles are present on the pedipalp femur, patella, and manus.
4. Lateral eye groups are reduced to a cluster of isolated lenses.
5. Median eyes are posterior to the lateral eyes.

Palaeopisthacanthus schucherti Petrunkevitch, 1913, is the only Palaeozoic scorpion which is known to have unequivocal intrasternite stigmata (Vogel and Durden 1966), and with *Compsoscorpius elegans* Petrunkevitch, 1949, it has reduced lateral eye clusters and posteriorly displaced median eyes. Kjellesvig-Waering (1986) noted the occurrence of trichobothria in *Palaeopisthacanthus*, but the pedipalps of *Compsoscorpius* are incompletely known and he was unable to determine whether trichobothria are present.

An examination of the available body fossils has confirmed Kjellesvig-Waering's observations. More importantly, small fragments of tergite cuticle are still present in the type material of *Compsoscorpius*, and this is identical in its cuticle characteristics to the material described here. *Palaeopisthacanthus* lacks preserved cuticle, but an excellent mould of the cuticle surface is present in the holotype, and it is clearly also of the same type. Kjellesvig-Waering (1986) did not note the similarity of cuticle ornament in *Palaeopisthacanthus* and *Compsoscorpius*. *Palaeopisthacanthus* is from the Mazon Creek fauna of Illinois. The fauna occurs in iron carbonate rich nodules from the Francis Creek Shale Member of the Carbondale Formation. Underlying the Francis Creek Shale is the Colchester (no. 2) Coal seam, and samples of the coal have yielded an abundant scorpion cuticle assemblage. Fragments of palaeopisthacanthid-type cuticle occur along with material attributable to several other Mazon Creek taxa.

Kjellesvig-Waering (1986) considered that *Palaeopisthacanthus* could be distinguished from *Compsoscorpius* on the basis of the shape of its carapace anterior margin. However, this structure is poorly preserved in all of the body fossils, so *Compsoscorpius elegans* Petrunkevitch, 1949, could justifiably be considered a junior synonym of *Palaeopisthacanthus schucherti* Petrunkevitch, 1913, with the minor differences between specimens noted by Kjellesvig-Waering (1986) possibly being due to intraspecific variation. However, the three known body-fossils of *C. elegans* all derive from a nodule fauna found *c.* 3 m above the Staffordshire Thick (or Main) Coal, in the Coseley district of England. The fauna is of Westphalian B age. Only one palaeopisthacanthid species was recognized in the English Carboniferous cuticle assemblages, also mostly of Westphalian B age, and since its trichobothrial distribution differs significantly from that of *P. schucherti*, the most parsimonious course of action available is to assign English palaeopisthacanthid material to *C. elegans*.

The Lone Star Lake assemblage from Kansas contains three species with palaeopisthacanthid-type cuticle. The most abundant of them has a trichbothrial distribution identical (as far as it is known) to *Compsoscorpius*, but other characters suggest that it does not belong in that genus, therefore it is described below as *Cryptoscorpius americanus* gen. et sp. nov. The other species are represented by single specimens of the pedipalp manus and fixed finger. One of these has been attributed to a new species of *Palaeopisthacanthus*, and the other has a number of unique characters which exclude it from any of the genera cited above, and is therefore described here as *Corniops mapesii* gen. et sp. nov.

PHYLOGENETIC RELATIONSHIPS

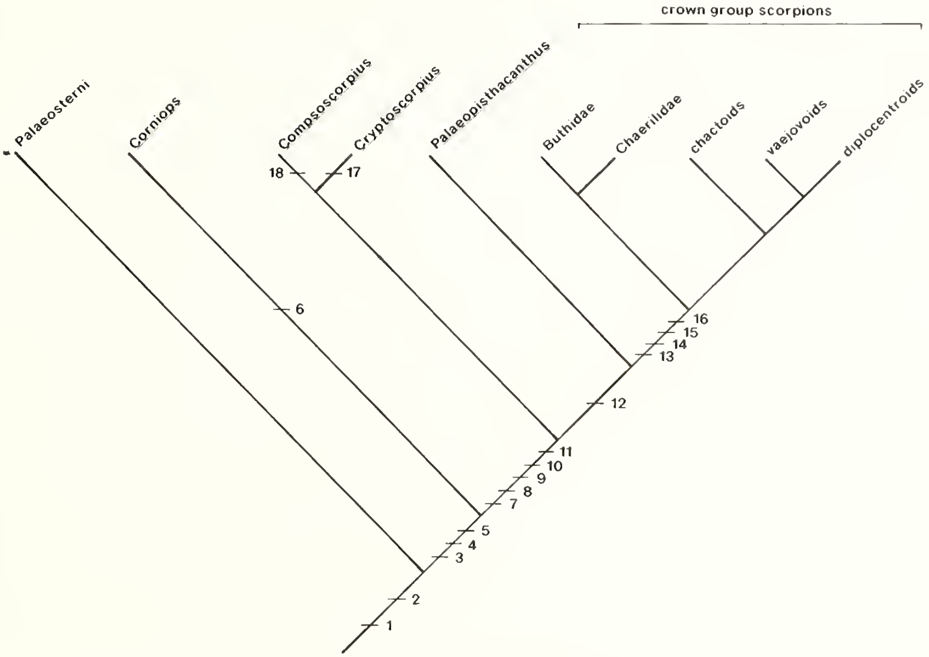
Previous work

Kjellesvig-Waering (1986) placed the Palaeopisthacanthidae in his sub-order Neoscorpionina, primarily because he believed them to be the only Palaeozoic scorpions with book-lungs rather than gills, but also because he observed just three ocelli in each lateral eye group. However, it has been argued on the basis of functional morphology and palaeophysiology that most Palaeozoic scorpions were fully terrestrial and possessed book-lungs (Selden and Jeram 1989; Stockwell 1989). Direct evidence of book-lungs in a Lower Carboniferous scorpion which lacks intrasternite stigmata has also been described (Jeram 1990).

Stockwell (1989) sought to integrate the systematics of fossil and Recent scorpions, which had developed largely independently of each other. In doing so, he expanded the Neoscorpionina to include fossil forms with reduced lateral eye groups and with the two posterior pairs of coxae abutting the sternum. He achieved this by creating a new infraorder, the Palaeosterni, which essentially consists of the Eoctonoidea (*sensu* Kjellesvig-Waering 1986). The Palaeosterni lack intrasternite stigmata, but Stockwell (1989) followed Kjellesvig-Waering, and others, in assuming that they had marginal stigmata, although there is no convincing evidence that they are present in any eoctonoid (Wills 1960; Selden and Jeram 1989). Stockwell (1989) considered *Palaeopisthacanthus* and *Compsoscorpius* to be genera *incertae sedis* within the infraorder Orthosterni, in which were also included the four Recent superfamilies he recognized; the Buthoidea, Chactoidea, Vaejovoidea, and Scorpionoidea. Stockwell's (1989) revision of Recent scorpion classification was based on an exhaustive cladistic analysis of all non-buthid genera, employing 138 binary characters. His conclusions differ from those of less thorough cladistic treatments (e.g. Lamoral 1980), but it remains to be seen if they will be widely accepted by neontologists.

Cladistic analysis

New characters revealed by the palaeopisthacanthid-type cuticles allow the position of this group to be determined relative to the Recent superfamilies. The cladogram given in Text-figure 1 is based on that of Stockwell (1989, fig. 251), but additional characters supporting the proposed palaeopisthacanthid groupings are supplied. Synapomorphies for the groupings of Recent scorpions are provided by Stockwell (1989) and are not repeated here. It should be noted that *Palaeopisthacanthus*, *Compsoscorpius*, and *Cryptoscorpius* gen. nov. are incompletely known, whilst *Corniops* gen. nov. is represented by a single pedipalp manus. Since it is the relationship between the palaeopisthacanthids and Recent scorpions that is of interest, only characters which might shed light on that relationship are considered here. *Gymnoscorpius* gen. nov. is not included in the cladogram.



TEXT-FIG. 1. Cladogram illustrating relationships between fossil orthostern taxa and Recent scorpion clades. Numbered autapomorphies supporting the groupings of taxa in the cladogram are discussed in the text.

The Palaeosterni are regarded as the sister group of the Orthosterni and recognition of autapomorphies for the suborder (Paleosterni + Orthosterni) was achieved by outgroup comparison with all other Palaeozoic scorpions. The Orthosterni show three important character state transition series which provide most of the taxonomically useful character states listed below:

1. Reduction of number of ocelli in lateral eye groups.
2. Increase in trichobothrial numbers.
3. Reduction in number of cheliceral teeth (reversal).

Particular emphasis is placed on trichobothrial character states because of their importance in Recent scorpion taxonomy (Sissom 1990), and the variability of this character in the fossil material.

Discussion of characters

The characters employed are listed below and followed by the plesiomorphic state, the derived state, and a brief discussion of each character.

1. Lateral ocelli (a): 'compound' lateral eyes, or, dispersed lateral ocelli, with ten or fewer ocelli in each lateral eye group. 'Compound' lateral eyes like those of eurypterids occur in all Palaeozoic scorpions except the Neoscorpionina, in which the eyes are reduced to ten or fewer isolated ocelli. Preservation rarely allows the lateral eyes to be studied in detail, and although many fossil scorpions appear to lack them (Petrunkevitch 1949; Kjellesvig-Waering 1986), their loss has only been conclusively demonstrated in some Triassic mesophonids (Wills 1947).
2. Preanal segment: short, or, long. Palaeosterni and Orthosterni have a preanal segment which is significantly longer than the preceding metasomal segment. In all other fossil scorpions the preanal segment is shorter than, or approximately equal in length to, the preceding metasomal segment.
3. Cuticle ornament: non-palaeopisthacanthid-type, or, palaeopisthacanthid-type.
4. Chelal trichobothria (a): trichobothria absent, or, trichbothria present. The presence of pedipalpal trichobothria is regarded here as a synapomorphy for the Orthosterni (*Corniops* gen. nov., +palaeopisthacanthids + Recent families). They have not been positively identified in any other fossil scorpions.
5. Pedipalp dentition (a): palaeostern-type, or, orthostern-type. The pedipalp dentition of modern scorpions and palaeopisthacanthids consists of simple thorn-like teeth arranged in rows along the opposed faces of the pedipalp fingers. With the exception of juveniles, in which the dentition is similar to that of Recent scorpions (unpublished observations), all other fossil scorpions in which dentition is known have rows of large follicles, within which are set sclerotised conical teeth (see Wills 1947, pl. 9, figs 1–6; 1960, pl. 50, fig. 3). The dentition of orthostern-type may have been derived by the neotenic retention of juvenile palaeostern dentition in orthostern adults.
6. Pedipalp dentition (b): main denticle row divided into primary sub-rows, or, single continuous denticle row. The Palaeosterni, Palaeopisthacanthidae, and nearly all Recent scorpions, have a main denticle row composed of discrete primary sub-rows. The single continuous denticle row of *Corniops* gen. nov. is therefore probably an autapomorphy for that genus.
7. Cheliceral dentition (a): no internal teeth, or, five internal teeth. Cheliceral dentition is a taxonomically useful character in Recent scorpions (Vachon 1963) but the preservation of fossils is rarely good enough for their dentition to be described accurately. However, the cheliceral dentition of palaeopisthacanthids is unique among scorpions, living or fossil. The presence of five internal teeth on the fixed finger is a palaeopisthacanthid autapomorphy. Internal teeth are unknown in other fossil scorpions, but a single internal tooth is present in Recent buthids, and a pair in some chactoids. A character state transition series leading to the reduction of cheliceral teeth on both the fixed and movable fingers could account for the states present in each of the Recent scorpion families. It is also notable that the palaeopisthacanthid state, plesiomorphic with respect to Recent families (Stockwell 1989), shows little size differentiation of teeth. The notation developed by Vachon (1963) for cheliceral dentition assumes the homology of certain teeth in different families. However, if Recent scorpion dentitions have been derived by reduction in number and size differentiation from the plesiomorphic state, then the assumption of homology should be viewed with caution, and it may be necessary to reassess cheliceral dentition in Recent families in the light of fossil evidence.
8. Lateral ocelli (b): lateral ocelli all approximately of same size, or, major and minor ocelli present. Lateral ocelli of palaeopisthacanthids and some Recent scorpions show size differentiation

into major and minor ocelli (Text-fig. 8B; González-Sponga 1977). Size differentiation has not been observed in other fossil scorpions or eurypterids.

9. Intrasternite stigmata: absent, or, present. Intrasternite stigmata are present in all Recent scorpions and palaeopisthacanthids. Marginal stigmata are known in *Mesophonus* (*sensu* Wills 1947), and have been postulated in some Palaeozoic scorpions (Kjellesvig-Waering 1986). However, none of the Palaeozoic cases is convincing, and where the ventral mesosomal anatomy is well known, stigmata are certainly absent (Wills 1960). The presence of intrasternite stigmata is therefore a synapomorphy for the Palaeopisthacanthidae + Recent families, and the marginal stigmata of *Mesophonus* are almost certainly independently derived (see also Jeram 1994).

10. Chelal trichobothria (b): pedipalp manus lacking Et trichobothria, or, pedipalp manus with Et trichobothria.

11. Metasomal segments: Anterior transverse ridge absent, or, anterior transverse ridge present. Metasomal segments of palaeopisthacanthids all have an anterior transverse ridge (like that present on mesosomal tergites) around the circumference of the sclerite. A limited survey of Recent scorpions revealed that it is present in some genera (e.g. *Ananteris*, *Lychas*, *Euscorpius*, *Pandinus*) but only on the ventral surface of the first, and sometimes second, metasomal segment. In other genera (e.g. *Broteochactus*) it is absent. This character is not present in the Palaeosterni, or in other fossil scorpions where the metasoma is known in detail, and therefore is a synpomorphy for the Palaeopisthcanthidae + Recent families.

12. Chelal trichobothria (c): No Eb trichobothria on manus, or, two or more Eb trichobothria on manus. The addition of Eb trichobothria on the manus of *Palaeopisthacanthus* is shared with all Recent scorpions, where there are three Eb trichobothria in each of the fundamental patterns.

13. Cheliceral dentition (b): Five internal teeth on fixed finger, or, one or none internal teeth (reversal). See notes for character 7 above.

14. Lateral ocelli (c): more than five lateral ocelli, or five or fewer lateral ocelli. Recent scorpions have two to five lateral ocelli in each lateral eye group. This reduction in number serves as a synapomorphy for the Recent scorpion families.

15. Chelal trichobothria (d): only eb trichobothrium on fixed finger, or, trichobothria present on fixed finger in addition to eb. Vachon (1973) recognized three 'fundamental' patterns of trichobothrial distribution in Recent scorpions. The three 'fundamental' patterns themselves share an underlying pattern common to them all which, it might be reasonably hypothesized, represents the plesiomorphic state with respect to the Recent scorpion families. Using the notation proposed by Vachon (1973), the following chelal trichobothria are common to all three distributions; $Eb_{(1-3)}$, V_1, Et, Est, Esb, it, db, dt, et, est, eb, esb. The overall polarity of this character state transition series is toward the addition of trichobothria, although rare trichobothrial losses are also known (e.g. Franke and Soleglad 1981). The palaeopisthacanthid pattern is very much less derived than any of the modern chelal distributions. Furthermore, the latest common ancestor of all modern scorpion families probably also had a considerably more derived chelal pattern than the palaeopisthacanthids. The hypothetical distribution for this ancestor is; $Eb_{(1-3)}$, Esb, Est, Et, $V_{(1-4)}$, it, ib, db, dt, et, est, eb, esb. From this, the type A pattern (Buthidae) could be derived by the loss of $V_{(3-4)}$ and ib; the type B pattern (Chaerilidae) by the loss of $V_{(2-4)}$; and the type C pattern (all other Recent families) by the addition of $Et_{(2-4)}$, Dt, Dst, and dsb.

It might be argued that either the type A or type B pattern is the most primitive, and that the others are derived from it, but as the palaeopisthacanthids possess four ventral trichobothria on the manus, this should be regarded as the plesiomorphic state, and the loss of ventral trichobothria is a derived state in the Buthidae and Chaerilidae. Furthermore, it would be a very remarkable case of parallelism indeed if all three Recent distributions were derived independently from a palaeopisthacanthid-type distribution, since with fourteen common trichobothria there is a high degree of congruency between them. Although these arguments have only been applied to the chelal trichobothria, similar cases can be made for the derivation of femural and patellar trichobothria. For the purposes of this analysis, the derived state is most simply characterized by the presence of trichobothria on the fixed finger, in addition to the eb trichobothrium.

16. First mesosomal sternite: short, or, long. In palaeopisthacanthids and the Palaeosterni the first mesosomal sternite is shorter than the second. All Recent scorpions have a sub-trapezoidal first sternite which is longer than the more rectangular second sternite.

17. Pedipalp fingers: longer than manus, or, equal to manus. In the plesiomorphic state the pedipalp fingers are longer than the manus. In *Cryptoscorpius* gen. nov. the fingers are approximately equal in length to the manus. Although many Recent genera have short fingers, this character appears to have originated independently many times, and in this case it can be regarded as an autapomorphy for *Cryptoscorpius* gen. nov. within the Palaeopisthacanthidae.

18. Pedipalp secondary structures: absent, or, present. The presence of a tubercular secondary structure on the external face of the pedipalp manus in *Compsoscorpius* is regarded as an autapomorphy for the genus. Similar structures occur on the internal face in most Recent bothrurid males (Maury 1975), but they are not homologous and were independently derived.

Discussion. Results of the analysis are summarized in Text-figure 1. *Palaeopisthcanthus* emerges as the most crownward of the stem group plesions by virtue of the Eb trichobothria on its pedipalp manus, and an additional probable Et trichobothrium. The increased number of trichobothria on the pedipalp femur noted in one specimen (K14426) supports this, although only characters visible in the holotype of *P. schucherti* were utilized in the analysis. No uniquely derived characters were recognized in *Palaeopisthacanthus*. The other Carboniferous orthosterns are even more plesiomorphic with respect to the Recent scorpions. *Compsoscorpius* and *Cryptoscorpius* gen. nov. share a common trichobothrial distribution. Together they comprise the *Compsoscorpius* plesion. The genera are each supported by autapomorphies, but again the plesion as a whole has no uniquely derived characters. The position of *Corniops* gen. nov. as the least crownward plesion is determined by the apparently plesiomorphic state of its trichobothrial type and distribution. However, since only the partial pedipalp manus and fixed finger are currently known, it may ultimately be demonstrated that four of the five synapomorphies shared by the more crownward taxa were also shared by *Corniops* gen. nov. If this were the case, it would still not effect the position of *Corniops* gen. nov. as the most plesiomorphic of the orthosterns. The pedipalpal dentition of *Corniops* gen. nov. is an autapomorphy of the genus. Synapomorphies supporting the groupings of Recent families and superfamilies in the cladogram are given by Stockwell (1989).

For the time being it is convenient to reserve the Carboniferous family Palaeopisthcanthidae, in which *Palaeopisthacanthus*, *Compsoscorpius*, and *Cryptoscorpius* gen. nov. are included, even though these genera do not share any uniquely derived characters. It would however not be appropriate to assign *Corniops* gen. nov. to the Palaeopisthacanthidae, or to establish a new family to accommodate it.

What is clear from the cladogram is that none of the Carboniferous orthosterns could be included in the crown group because the hypothetical last common ancestor of all Recent scorpions would have been significantly more derived than *Palaeopisthacanthus*. It is probable therefore that the crown group originated after the Late Carboniferous, but biogeographical evidence for the timing of origins of major Recent scorpion clades is somewhat ambiguous (e.g. Lamoral 1980; Stockwell 1989). The occurrence of palaeopisthacanthid-type cuticle fragments in Dinantian age shales overlying the East Kirkton Limestone at Bathgate, Scotland, pushes the probable origin of the orthostern scorpions back at least as far as the Early Carboniferous (Jeram 1994). Material which may represent a much older orthostern is present in the Middle Devonian Gilboa assemblage, but further study will be required to confirm the identity of these fragments.

At present no consensus exists amongst arachnologists concerning the systematic position of scorpions within the Chelicerata. However, in recent years there has been a general recognition that the class Arachnida is polyphyletic (Firstman 1973; Van der Hammen 1977; Weygoldt and Paulus 1979). Stockwell (1989) followed Van der Hammen (1977) in raising the Scorpionida to the status of a class. As a consequence more space is available in the taxonomic hierarchy for the grouping of fossil forms into monophyletic clades, thereby facilitating the integration of fossil and Recent scorpion classifications. In spite of the work of Kjellesvig-Waering (1986), there is still a long way to go before the systematics of fossil scorpions can be regarded as satisfactory. In the meantime the Palaeopisthacanthidae are not referred to any higher taxon within the Orthosterni, although it is hoped that the recognition and description of these plesiomorphic stem group taxa will facilitate a re-examination of Recent scorpion relationships and ultimately stabilization of their systematics.

SYSTEMATIC PALAEONTOLOGY

Class SCORPIONIDA Latreille, 1810
Order SCORPIONES Hemprich and Ehrenberg, 1837
Suborder NEOSCORPIONINA Thorell and Lindström, 1885
Infraorder ORTHOSTERNI Pocock, 1911

Emended diagnosis. Neoscorpionina with intrasternite stigmata. Pedipalpal trichobothria present.

Family PALAEOPISTHACANTHIDAE Kellesvig-Waering, 1986

Emended diagnosis. Orthosterni with four ventral trichobothria on the pedipalp manus, only eb trichobothrium on pedipalp fixed finger.

Genus PALAEOPISTHACANTHUS Petrunkevitch, 1913

Type species. Palaeopisthacanthus schucherti Petrunkevitch, 1913, from the Upper Carboniferous (Westphalian D) Francis Creek Shale of the Mazon Creek area, Illinois.

Emended diagnosis. Palaeopisthcanthidae with at least two Eb trichobothria on the pedipalp manus. Pedipalp fingers longer than manus.

Palaeopisthacanthus schucherti Petrunkevitch, 1913

Text-figure 2

1913	*Palaeopisthacanthus schucherti* Petrunkevitch, p. 48, pl. 2, figs 8–9; text-figs 11–12.
1949	*Palaeopisthacanthus schucherti* Petrunkevitch; Petrunkevitch, p. 154.
1953	*Palaeopisthacanthus schucherti* Petrunkevitch; Petrunkevitch, p. 33.
1955	*Palaeopisthacanthus schucherti* Petrunkevitch; Petrunkevitch, p. 43, text-fig. 43.
1966	*Palaeopisthacanthus schucherti* Petrunkevitch; Vogel and Durden, p. 655, pl. 81, figs 1–3; text-figs 1–2.
1986	*Palaeopisthacanthus schucherti* Petrunkevitch; Kjellesvig-Waering, p. 232, text-figs 103–104.

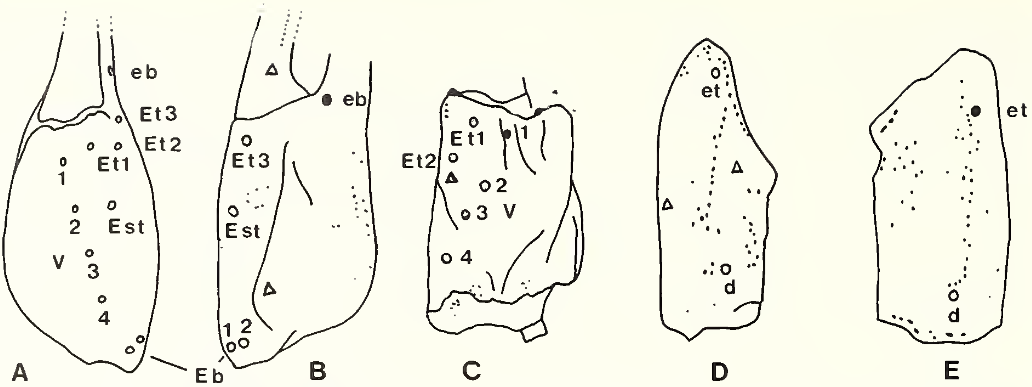
Holotype. Part and counterpart of a small ironstone nodule, YPM 140, containing the mould of a partially preserved scorpion, from the Francis Creek Shale of the Mazon Creek area, Grundy county, Illinois.

Additional material. See Appendix 1.

Emended diagnosis. As for genus, with three Et trichobothria positioned close to external condule

Discussion. The description of the holotype given by Kjellesvig-Waering (1986) was found to be reasonably accurate. However, several significant characters are redescribed here based on a re-examination of the holotype and additional material from the Colchester (no. 2) Coal (locality 7). Most aspects of Kjellesvig-Waering's (1986) description were confirmed, and are not repeated here.

Carapace. Kjellesvig-Waering (1986, p. 232) diagnosed *Palaeopisthacanthus* as having a 'strongly-cuspidate anterior margin'. The appearance of a cuspidate anterior margin may be illusory, due to the bowing of the carapace anterior margin over the chelicerae in the fossil. The carapace shape is similar to that of *Cryptoscorpius* gen. nov. and *Compsoscorpius*. Vogel and Durden (1966) correctly



TEXT-FIG. 2. *Palaeopithacanthus schucherti* Petrunkevitch, 1913. YPM 140, holotype; Francis Creek Shale (Westphalian D); Mazon Creek, Illinois. A, reconstruction of chelal trichobothrial distribution, viewed from inferior side. B, left chela, exterior surface. C, left chela, interior surface. D, left pedipal patella, superior surface. E, right pedipalp femur, superior surface. Figures B–E after Kjellesvig-Waering (1986, text-fig. 104). In figures B–E, triangles indicate trichobothria identified by Kjellesvig-Waering but not confirmed by this study; filled circles are trichobothria not noted by Kjellesvig-Waering; open circles are trichobothria noted by Kjellesvig-Waering and confirmed in this study.

observed three large lateral ocelli on each side of the carapace. These are located on raised eye nodes, and it is possible that minor ocelli are also present, but cannot be reliably differentiated from cuticular tubercles in the mould.

Coxal apophyses. The apophyses of the first two pairs of walking-leg coxae are not well-preserved in the holotype. The anterior tips of both pairs have broken away, and what appeared to Kjellesvig-Waering (1986) to be a *Chaerilus*-like spatulate apophysis on the anterior coxa is probably part of the underlying pedipalpal coxa. A pair of apophyses from the Colchester (no. 2) Coal (K14422) are identical in structure to those of *Cryptoscorpius* gen. nov. (Pl. 6, fig. 1; Text-fig. 8A).

Sternum. Kjellesvig-Waering (1986, text-fig. 103) interpreted the sternum as occupying the entire area between the three posterior pairs of coxae. However, an alternative interpretation of the fossil is possible. The illustrations of Vogel and Durden (1966, pl. 8, fig. 2; text-fig. 2) show a convex anterior margin which is easily visible in the specimen. The triangular area anterior to this which Kjellesvig-Waering (1986) interpreted as an anterior portion of the sternum may simply be due to the post-mortem separation of the second pair of coxae. If this interpretation is correct, then the sternum is sub-pentagonal with convex anterior and lateral margins, and is wider than long.

Sternites. Vogel and Durden (1966) found only three stigmata-bearing sternites on the ventral surface of the abdomen. Kjellesvig-Waering (1986) reported a fourth sternite anterior to these, although the presence of stigmata on the anterior sternite was not confirmed by this study because

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EXPLANATION OF PLATE 1

Figs 1–9. *Compsoscorpius elegans* Petrunkevitch, 1949. See Appendix 1 for localities. All specimens Upper Carboniferous (Westphalian B). 1, K14475; mesosomal tergite 5 from same specimen as figure 3; ×26. 2, K14504; posterior mesosomal tergite; ×26. 3, K14475; partial mesosoma; see Text-figure 3A for explanation; ×26. 4, K14433; postabdominal segment; see Text-figure 3C for explanation; ×26. 5, K14472; right side of sternite; see Text-figure 3F for explanation; ×4. 6, K14533 sternite fragment; see Text-figure 3D for explanation; ×42. 7, K14481; preanal segment; see Text-figure 3B for explanation; ×26. 8, K14570; postabdominal segment, ventral surface in centre; see Text-figure 3E for explanation; ×26. 9, K14517; see Text-figure 3G for explanation; ×26.

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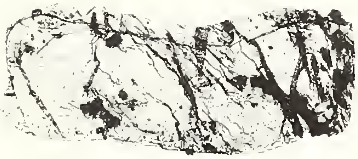
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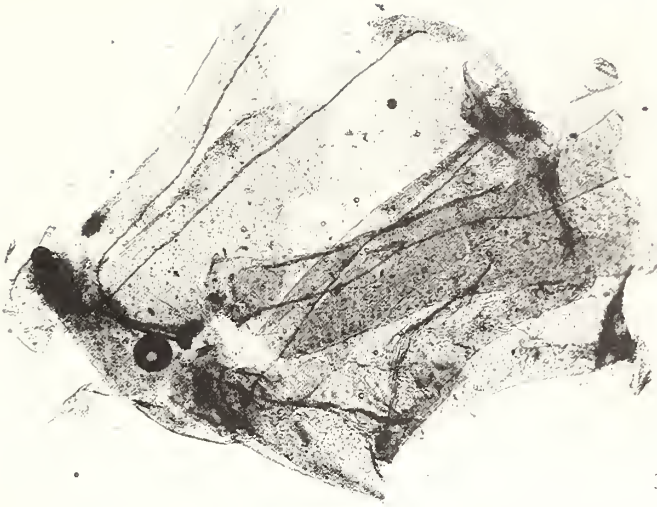
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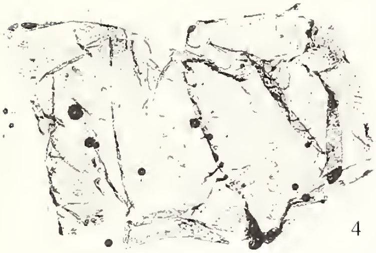
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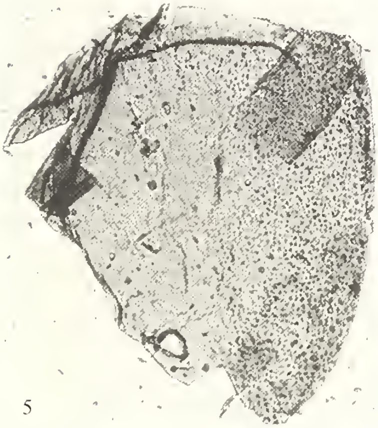
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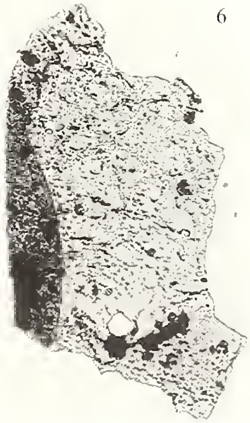
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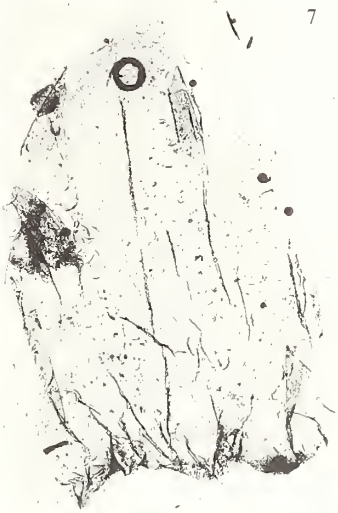
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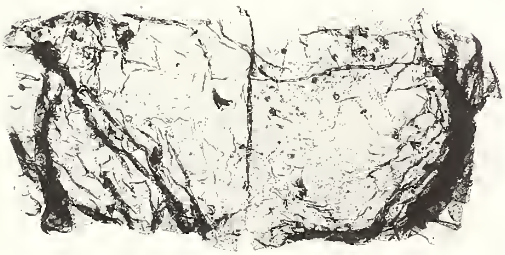
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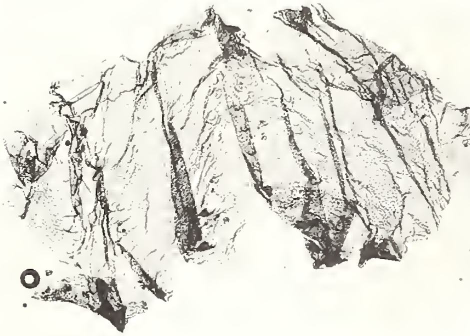
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JERAM, *Compsoscorpius*

preservation in this area of the holotype is poor. The anterior sternite is very short, contrasting with Recent scorpions, in which the anterior sternite is elongated relative to the others.

Pedipalps. Kjellesvig-Waering (1986) stated that the pedipalp fingers lack denticles, but a row of denticles can be seen towards the base of the free finger of the left pedipalp of the holotype. The apparent absence of dentition on the fingers is due to post mortem distortion and folding of the cuticle which has obscured the cutting edges almost entirely. Trichobothrial follicles (bothria) are preserved as mushroom-shaped bosses on the internal mould, due to sediment infilling the cup-like bothria. Setal follicles are much smaller, and are preserved as simple round scars on the mould. The trichobothrial distribution of *P. schucherti* is shown in Text-figure 2. Most of the bothria noted by Kjellesvig-Waering (1986) were confirmed, but a few features are definitely not bothria, some are equivocal, and a few additional bothria were located. The pedipalp femur of the holotype reveals a single d bothrium, and a possible et bothrium. The patella also has one d and one et bothrium. Two other bothria figured by Kjellesvig-Waering (1986, text-fig. 104E) could not be located with certainty. Chelal trichobothria are similar to those of other palaeopisthacanthids described below, with some additions. Four ventral, three Et, and two Eb bothria are present. An additional Eb bothrium may have been present in life, but the crumpled preservation of the holotype's cuticle surface means that it is unlikely that all the original trichobothria will be determinable, particularly on the poorly preserved left pedipalp. Two bothria figured by Kjellesvig-Waering (1986) are inconclusive, and the supposed bothrium on the free finger is a large pyrite granule (Text-fig. 2B).

Palaeopisthacanthus vogelandurdeni sp. nov.

Plate 5, figure 4; Plate 7, figure 6; Text-figure 6D

Derivation of name. The species name is in honour of Beatrice Vogel and Christopher Durden who first recognized the close relationship of *Palaeopisthacanthus* to Recent scorpions.

Holotype. Fixed finger and distal portion of a pedipalp manus, K14086, from cuticular shales immediately overlying the Lower Williamsburg Coal, at Lone Star Lake, Kansas.

Additional material. The Lone Star Lake assemblage probably contains additional fragments belonging to this species, but at present they cannot be reliably differentiated from those of *Cryptoscorpius mapesii* gen. et sp. nov.

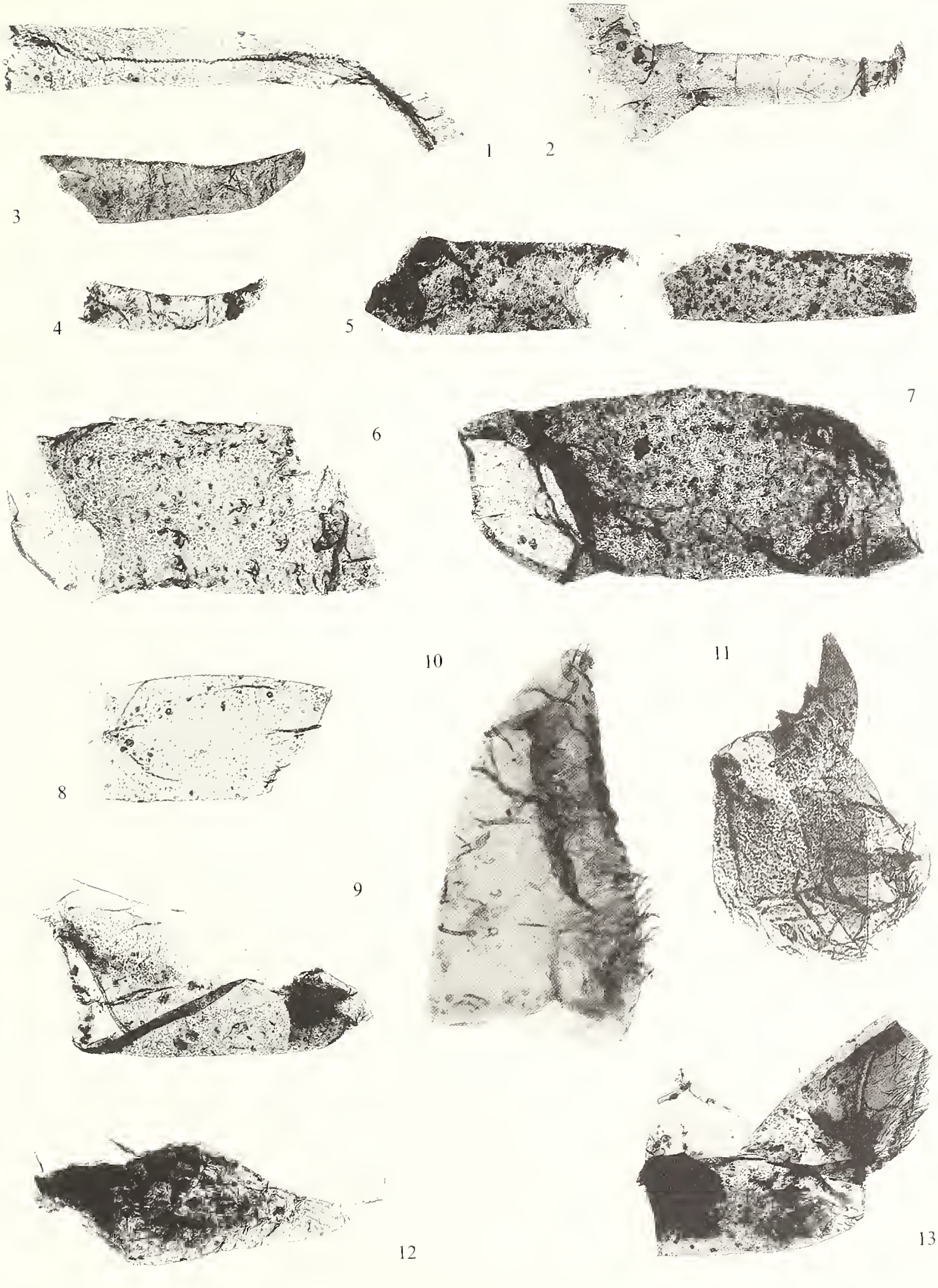
Diagnosis. Pedipalp fingers longer than manus. Primary denticle row consisting of seven primary sub-rows, each containing twelve to fourteen denticles. Et trichobothrium positioned approximately half way across the external face of the manus.

EXPLANATION OF PLATE 2

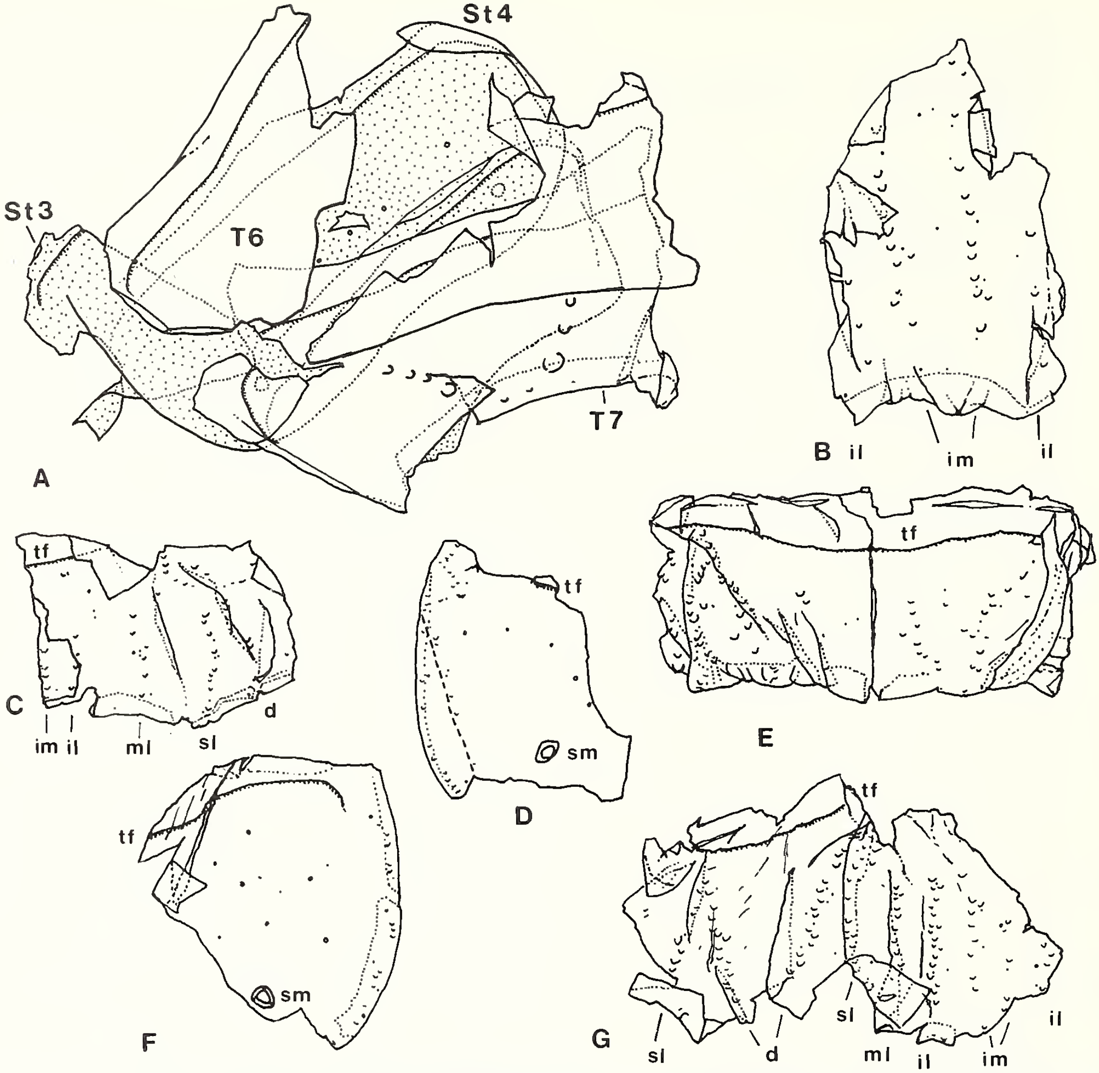
Figs 1–7, 10–13. *Compsoscorpius elegans* Petrunkevitch, 1949. See Appendix 1 for localities. 1–2, 4–7, Upper Carboniferous (Westphalian B); 3, Upper Carboniferous (Westphalian A). 1, K14485; pedipalp free finger; × 32. 2, K14490; partial pedipalp manus and fixed finger; see Text-figure 4A–B for explanation; × 32. 3, K14428; partial pedipalp finger; × 32. 4, K14500; juvenile pedipalp finger; × 32. 5, K14432; two fragments from an adult pedipalp free finger; × 26. 6, K14460; pedipalp patella; see Text-figure 3F for explanation; × 32. 7, K14566; adult pedipalp patella, see Text-figure 3C for explanation; × 26. 10, K14564; chelicera free finger, external row of teeth in centre; × 64. 11, K14546; 'chelicera' manus with fixed finger; see Text-figure 3E for explanation; × 42. 12, K14571; vesicle and aculeus, proximal end obscured by opaque organic matter; × 26. 13, K14499; coxa of walking-leg 2 with apophysis; × 32.

Figs. 8–9. *Cryptoscorpius americanus* gen. et sp. nov.; Lone Star lake, Kansas; Upper Carboniferous (Stephanian B). 8, K14402; juvenile pedipalp femur with three superior trichobothria; see Text-figure 3D for explanation; × 39. 9, K14098; coxa of walking leg 3; × 26.

PLATE 2

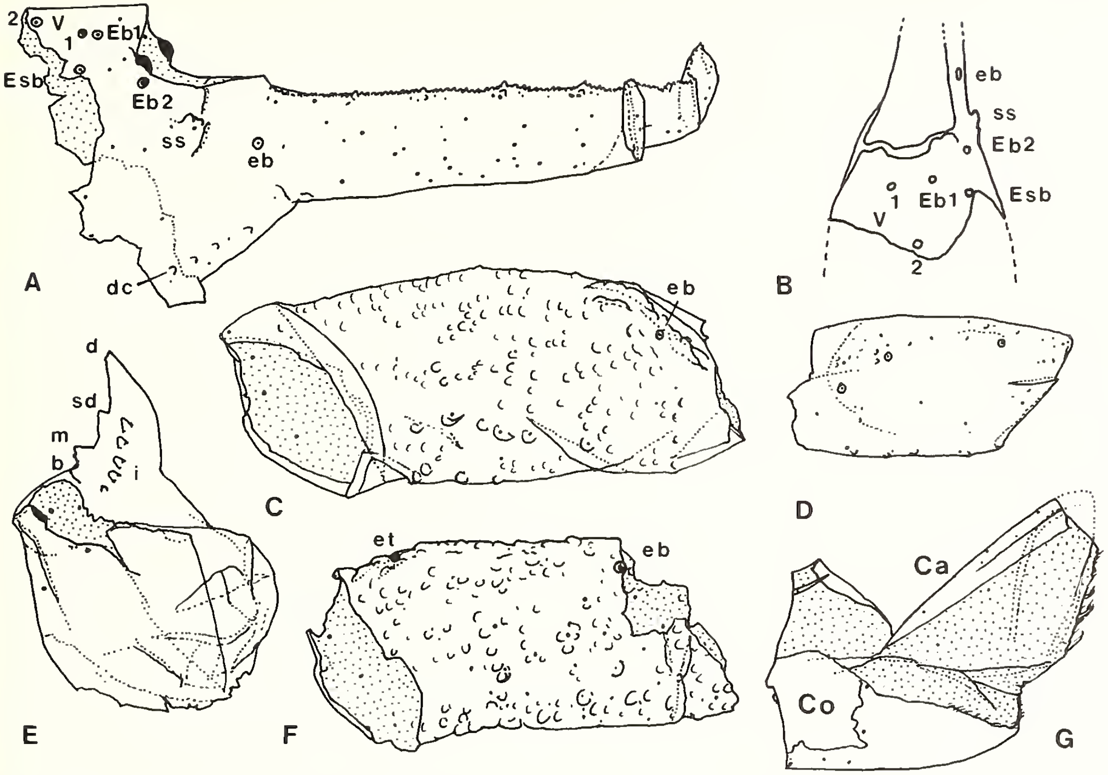


JERAM, *Compsoscorpius*, *Cryptoscorpius*



TEXT-FIG. 3. *Compsoscorpius elegans* Petrunkevitch, 1949. Explanatory drawings for specimens illustrated in Plate 1. All specimens from the Westphalian B of England; see Appendix for details of locality and horizon for individual specimens. See Plate 1 for scale. A, K14475; partial abdomen viewed from dorsal side; tergite 6 is torn into two large fragments and overlies tergite 7; these overly sternite 4, in which the right stigma is clearly visible; a small fragment of sternite 3 is present on the far left. B, K14481; ventral surface of preanal segment, showing inferior median and inferior lateral carinae. C, K14433; right half of metasomal segment opened out to display dorsal surface on right and ventral on left. D, K14533; fragment of large sternite, the folded lateral margin has been restored to its original position in the drawing. E, K14570; metasomal segment, opened out to display ventral surface in centre and dorsal surface on either side. F, K14472; sternite fragment viewed from ventral side. G, K14517; metasomal segment opened out to display dorsal surface on left and ventral on right. Abbreviations and conventions are given in 'Methods' in the text.

Description. The fixed finger is long and slender, and although only a distal portion of the manus is preserved it is clear that the finger was considerably longer than the manus in life, like that of *P. schurcherti.* The cuticle of the manus is finely tuberculate, but the distal two-thirds of the fixed finger lack ornament. A prominent dorso-interior marginal carina is present, and two further carinae are visible on the portion of the exterior



TEXT-FIG. 4. *Compsoscorpius elegans* Petrunkevitch, 1949 (A–C, E–G) and *Cryptoscorpius americanus* gen. et sp. nov. (D). Explanatory drawings for specimens illustrated in Plate 2. All specimens of *C. elegans* are from the Westphalian B of England; *C. americanus* gen. et sp. nov. is from Lone Star Lake, Kansas (Stephanian B). See Appendix for details of localities and horizons, and Plate 2 for scale. A, K14490; distal end of pedipalp manus and fixed finger, viewed from exterior side, dorsal surface at bottom. B, reconstruction of trichobothrial distribution on K14490; viewed from inferior side. C, K14566; pedipalp patella viewed from inferior prolateral side; et bothrium is not visible due to opaque detritus. D, K14402; pedipalp femur from juvenile with three superior bothria, viewed from superior side. E, K14546; cheliceral hand and fixed finger viewed from inner side. F, K14460; pedipalp patella viewed from inferior prolateral side, proximal end missing. G, K14499; coxa of leg 2 showing broad apophysis with filtering mat of setae, distal end missing, viewed from inner side. Abbreviations and conventions are given in 'Methods' in the text.

surface preserved (Pl. 5, fig. 4). Applying the nomenclature of Stahnke (1970), the superior of this pair is an inner secondary carina, and the inferior, a digital carina. Two bothria are present on the holotype. The eb bothrium is remarkable as the only example of palaeopisthacanthid trichobothrium in which the hair is still present (Pl. 5, fig. 4). The hair lies between the opposed layers of cuticle and owes its preservation to having been pushed inwards into the lumen of the sclerite. The other is an Et bothrium lying approximately half way across the external surface on the digital carina. Although the manus is incomplete, it is certain that no external trichobothria lie distally to this one on the manus, and therefore Et is the most appropriate designation for it. However, it must be borne in mind that Vachon's (1973) terminology was devised for describing trichobothrial distributions in Recent scorpions, and that the terminology may not be able to accommodate all the potential variations in fossil material.

The dentition of the fixed finger consists of slightly oblique non-imbricated primary sub-rows. Excluding the most proximal sub-row, which is not complete in the holotype, twelve to fourteen denticles are present in each sub-row, the basal denticle in each being the largest. An internal accessory denticle lies just proximally to the basal denticle of each sub-row. There are no supernumary denticles (Pl. 7, fig. 6).

Discussion. The species is assigned to *Palaeopisthacanthus* because of its distinctive cuticle ornament and long pedipalp fingers. It can be distinguished from *P. schucherti* by the position of the Et trichobothrium. The absence of a secondary structure of the external face of the manus excludes it from *Compsoscorpius*.

Genus COMPSOSCORPIUS Petrunkevitch, 1949

Type species. Compsoscorpius elegans Petrunkevitch, 1949, from the Upper Carboniferous (Westphalian B) of Staffordshire, England.

Emended diagnosis. Palaeopisthacanthid with thirteen pedipalpal trichobothria, of which eight are chelal, three lie on the femur and two on the patella. Pedipalp fingers nearly twice the length of the manus. Chelal dentition of seven primary sub-rows, with twelve to fourteen denticles in each. Manus with large tubercular secondary structure on external face just posterior to the eb-trichobothrium.

Compsoscorpius elegans Petrunkevitch, 1949

Plate 1; Plate 2, figures 1–7, 10–13; Plate 3, figures 1–10; Plate 6, figures 4–7; Plate 7, figures 1, 5; Text-figures 3; 4A–C, E–G; 5A–J

1911 *Anthracoscorpio buthiformis* Pocock [*partim*], p. 26, fig. 7.
1949 *Typhlopisthacanthus anglicus* Petrunkevitch, p. 145, figs 143, 182.
1949 *Compsoscorpius elegans* Petrunkevitch, p. 149, figs 152, 154, 183–185.
1949 *Compsoscorpius elongatus* Petrunkevitch, p. 150, figs 147–150, 186–188.
1953 *Compsoscorpius elegans* Petrunkevitch; Petrunkevitch, p. 32.
1953 *Compsoscopius elongatus* Petrunkevitch; Petrunkevitch, p. 33.
1953 *Typhlopisthacanthus anglicus* Petrunkevitch; Petrunkevitch, p. 34.
1955 *Compsoscorpius elegans* Petrunkevitch; Petrunkevitch, p. 75, fig. 44.
1986 *Compsoscorpius elegans* Petrunkevitch; Kjellesvig-Waering, p. 236, text-figs 105–107.
1987 *Scorpionida incertae sedis* Bartram *et al.*, fig. 1.

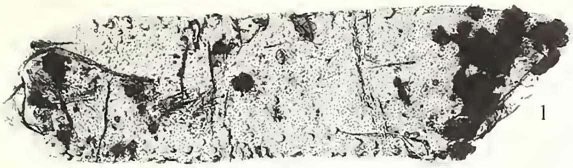
Holotype. BMNH 17883, part and counterpart of a small incomplete scorpion preserved in an ironstone nodule.

Additional material. BMNH In15862 and In31261. These are the holotypes of *C. elongatus* Petrunkevitch, and *Typhlopisthacanthus anglicus* Petrunkevitch respectively, which Kjellesvig-Waering (1986) considered to be junior synonyms of *C. elegans*. All three specimens are from shales above the Thick (or Main) Coal, in the Coseley district of Staffordshire, England. All are incompletely known from the dorsal surface only, and as no characters could be found to separate them, Kjellesvig-Waering's (1986) action seems justified.

EXPLANATION OF PLATE 3

Figs 1–10. *Compsoscorpius elegans* Petrunkevitch, 1949. See Appendix 1 for localities. All specimens Upper Carboniferous (Westphalian B). 1, K14488; femur of walking leg ?4; see Text-figure 4A for explanation; × 26. 2, K14458; femur of walking leg ?3; see Text-figure 4B for explanation; × 32. 3, K14565; patella of walking leg ?3; see Text-figure 4G for explanation; × 26. 4, K14496; tibia of leg 3 or 4; see Text-figure 4D for explanation; × 43. 5, 14484; basitarsus; see Text-figure 4H for explanation; × 32. 6, K14573; basitarsus; see Text-figure 4C for explanation; × 39. 7, K14498; distal end of tibia; see Text-figure 4F for explanation; × 39. 8, K14510; basitarsus; see Text-figure 4E for explanation; × 39. 9, K14480; basitarsus; see Text-figure 4J for explanation; × 39.

Figs 11–16. *Gymnoscorpius mutillidigitus* gen. et sp. nov. See text for localities, all specimens Upper Carboniferous (Westphalian B). 11, K14491; large pedipalp patella, note groups of slit sensilla at distal end; × 26. 12, K14578; paratype, partial pedipalp manus and fixed finger of large individual; × 32. 13, K14497; holotype, pedipalp manus with fixed and free fingers; × 39. 14, K14506; metasomal segment; see Text-figure 4K for explanation; × 32, 15, K14576; metasomal segment; see Text-figure 7L for explanation; × 32. 16, K14575; vesicle and aculeus; see Text-figure 4M for explanation; × 32.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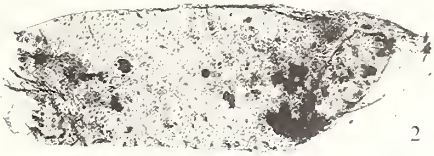
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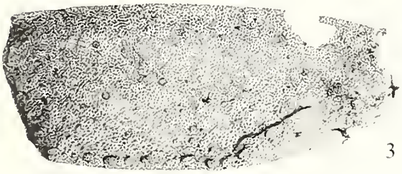
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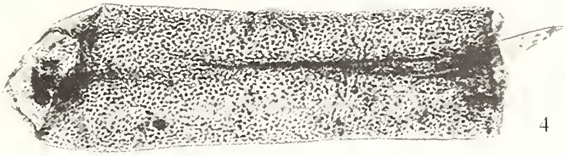
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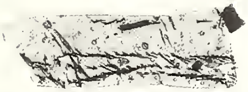
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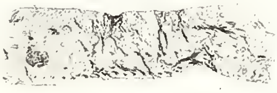
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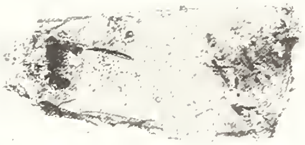
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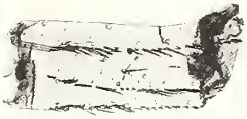
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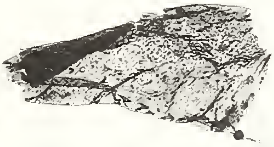
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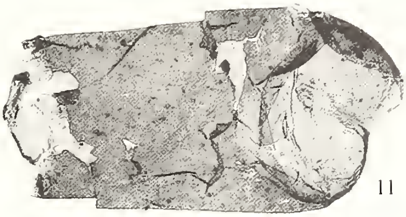
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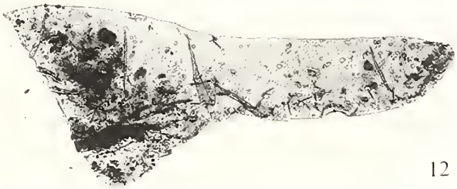
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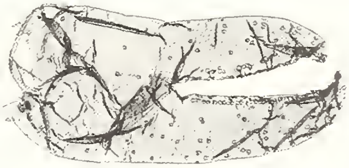
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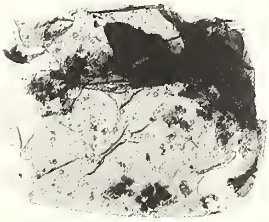
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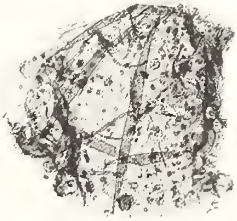
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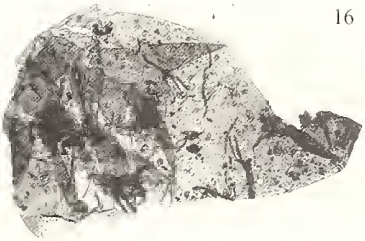
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JERAM, *Compsoscorpius*, *Gymnoscorpius*

Dispersed cuticle assemblages containing palaeopisthacanthid-type cuticle have been obtained from several localities in England. Details of these are given above. All of the English palaeopisthacanthid material has been referred to *C. elegans* because only one species can be recognized in the assemblages, and this cannot be reliably distinguished from *C. elegans* which is poorly known. The cuticle material is listed in the Appendix.

Diagnosis. As for genus.

Description. Carapace. An examination of the two specimens with lateral eyes preserved (BMNH I7883 and In15862) confirmed the presence of three major lateral ocelli. It is not possible to tell if minor ocelli are present or not. Unfortunately only a few carapace fragments were recognized in the cuticle assemblages, and none of these has lateral eyes preserved.

Abdomen. Tergites 1–6 lack carinae and are ornamented by evenly distributed small tubercles. Tubercles increase slightly in size posteriorly, and there is a posterior marginal row of bigger tubercles. Setae are sparse (Pl. 1, figs 1–2). The dorsal surface of tergite 7 bears two strong median carinae, delineated by larger tubercles, which converge posteriorly. A pair of weaker lateral carinae are present in large specimens, but are not well developed in juveniles (e.g. K14475). The ventral surface is probably also carinate, but no large specimens are known.

Several partial mesosomal regions were recovered (e.g. Pl. 1, fig. 3; Text-fig. 3A; Pl. 7, fig. 1) which include sternites with stigmata. Stigmata are circular, and slightly closer to the lateral margins than those of *P. schucherti*. Juvenile examples are devoid of ornament, whilst on larger specimens the typical tuberculose ornament is present marginally (Pl. 1, fig. 5). An anterior transverse ridge is present, but it is not produced posteriorly at the lateral margins (cf. tergites). A narrow doublure is present. Four sternites bearing stigmata were probably present in life, although the most complete of the partial specimens (Pl. 7, fig. 1) preserves only three.

Postabdomen. Metasomal segments are short, but increase slightly in length posteriorly along the tail. The fifth metasomal segment (preanal) is twice as long as the fourth (e.g. BMNH In 15862) and bears much weaker carinae than the others (Pl. 1, fig. 7; Text-fig. 3B). All metasomal segments have an anterior transverse ridge around their entire circumference, and posteriorly a doublure is present. Carinae are delineated by larger tubercles. Dorsal carinae are very prominent (e.g. Pl. 1, figs 8–9; Text-figs 3E, G), but pairs of superior-lateral, inferior lateral and inferior median carinae are also present, making a total of ten carinae per segment.

The vesicle is entirely smooth, except in the largest specimens which have typical palaeopisthacanthid ornament anteriorly. No carinae have been observed. The aculeus is relatively short, and is preserved as very thin pale cuticle. Towards its tip a pair of poison channels can be observed in well preserved specimens (e.g. Pl. 2, fig. 12). The cuticle of the vesicle bears pits approximately 8 μm in diameter and 10 μm deep. They appear as tiny tubercular structures on the inner surface of the fossil cuticle, and at the base of each is a 1 μm diameter pore which presumably connected with a cuticular duct in the inner exocuticle or endocuticle. These have not been observed in other palaeopisthacanthid sclerites, nor in any fossil scorpion cuticle except that of *Gymnoscorpius* gen. nov. (see below).

Prosomal appendages. The coxosternal arrangement is not known in its entirety although the apophyses of the first two pairs of walking-leg coxae are visible (but poorly preserved) in BMNH In31261 (Kjellesvig-Waering 1986, text-fig. 107). It is likely that the coxosternal structure is similar to that of *Palaeopithacanthus*,

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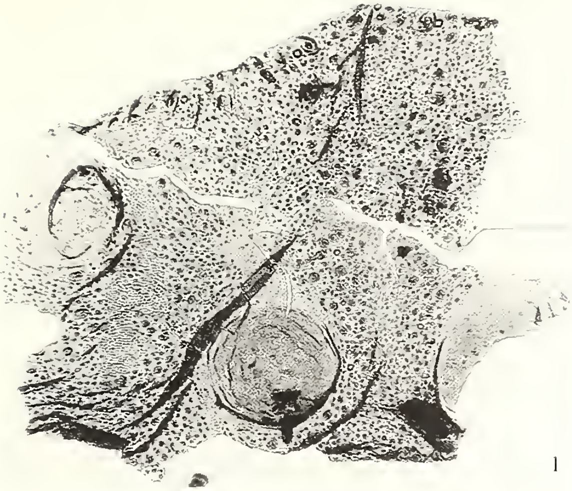
EXPLANATION OF PLATE 4

Figs 1–9. *Cryptoscorpius americanus* gen. et sp. nov. All specimens from Lone Star Lake, Kansas; Upper Carboniferous (Stephanian B). 1, K14413; two fragments of an adult carapace; see Text-figure 5A for explanation; ×43. 2, K14081; paratype, two fragments of a folded carapace; see Text-figure 5B for explanation; ×26. 3, K14080; paratype, folded carapace; see Text-figure 5C for explanation; ×26. 4, K14097 (right side) and K14100 (left); dorsal surface of mesosomal tergite 7; see Text-figure 5D for explanation; ×26. 5, K14410; left side of metasomal segment; see Text-figure 6H for explanation; ×26. 6, K14095; ventral surface of metasomal segment; see Text-figure 5E for explanation; ×26. 7, K14411; ventral surface (part) of metasomal segment; see Text-figure 5F for explanation; ×26. 8, K14096; metasomal segment; see Text-figure 5I for explanation, ×26. 9, K14099; right side of metasomal segment; see Text-figure 5G for explanation; ×26.

PLATE 4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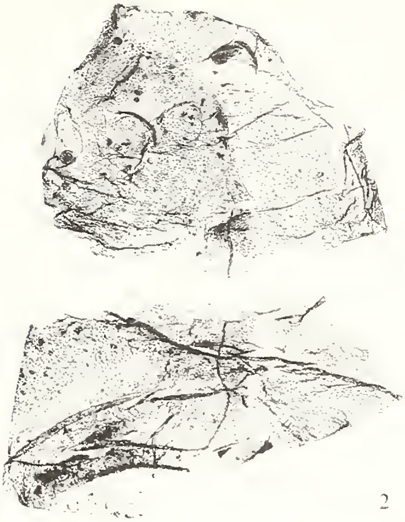
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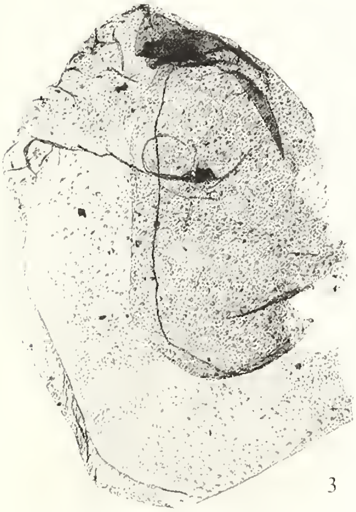
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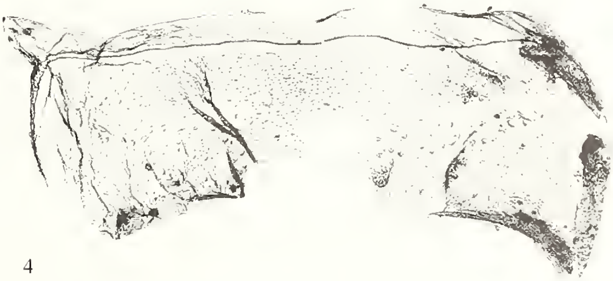
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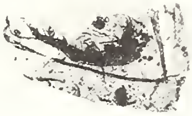
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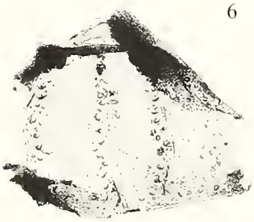
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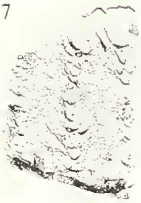

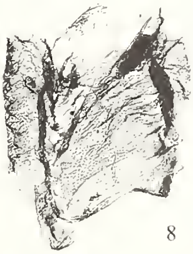
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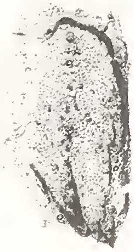
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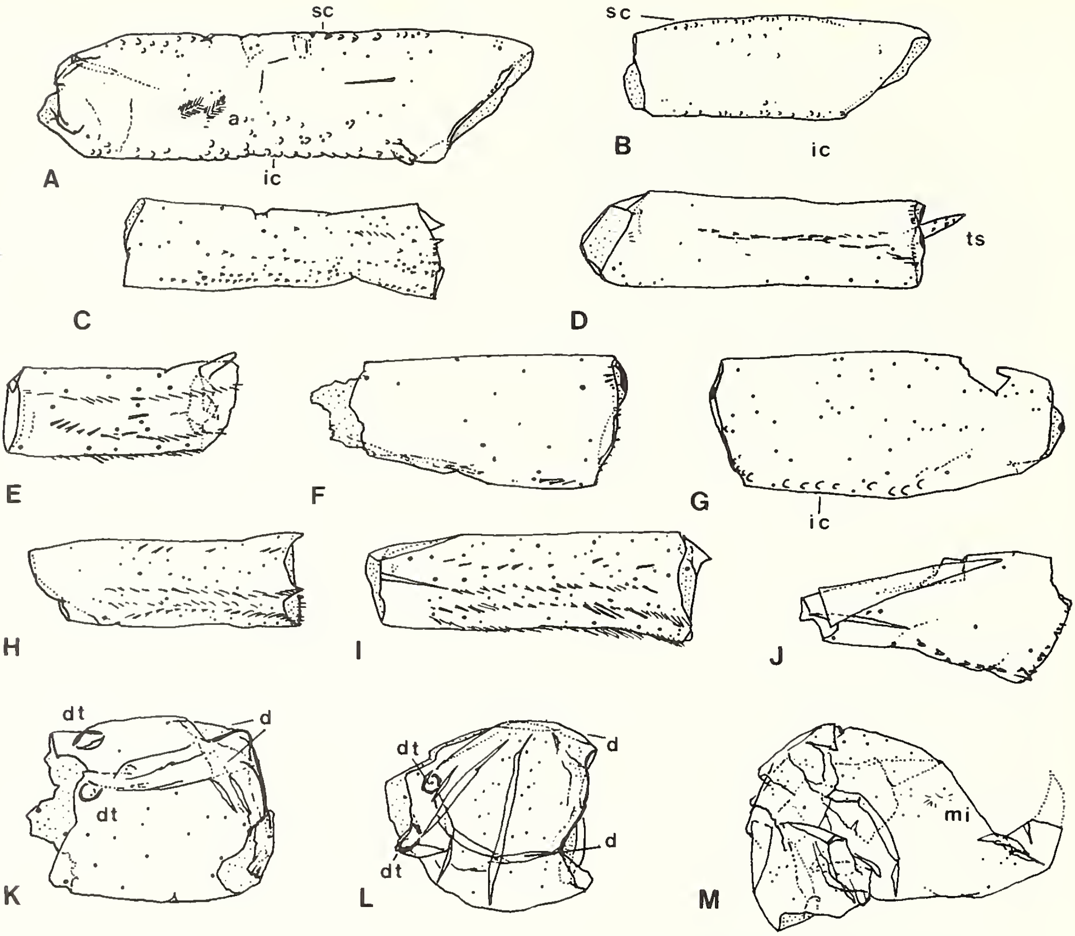
JERAM, *Cryptoscorpius*

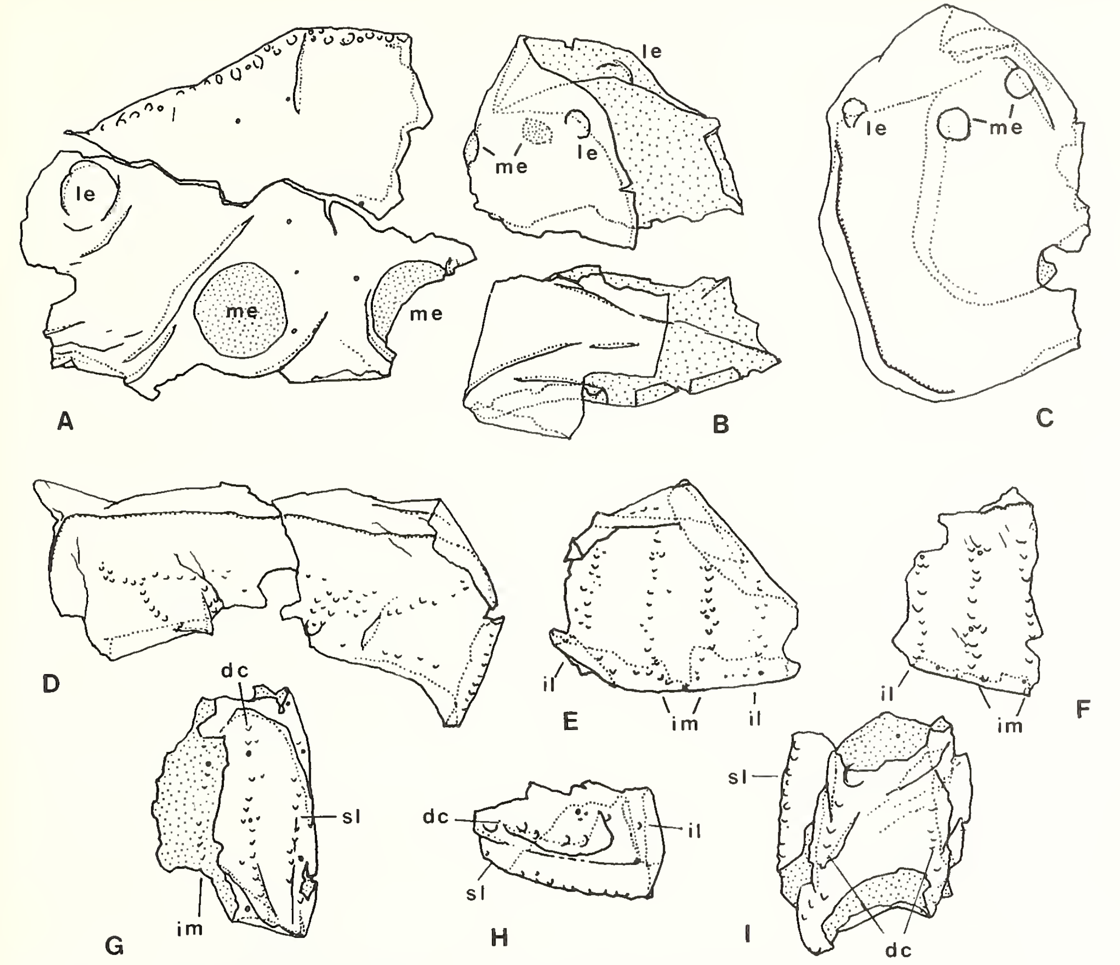


TEXT-FIG. 5. *Compsoscorpius elegans* Petrunkevitch, 1949 (A–J) and *Gymnoscorpius mutillidigitus* gen. et sp. nov. (K–M). Explanatory drawings for specimens illustrated in Plate 3. All specimens from the Westphalian B of England; see Appendix for details of localities and horizons. See Plate 3 for scale. A, K14488; femur of leg ?3, viewed from adaxial side. B, K14458; femur of leg ?2; viewed from adaxial side. C, K14573; basitarsus of posterior leg, viewed from prolateral side. D, K14496; tibia of leg 3 or 4, viewed from inferior side, note tibial spur. E, K14510; basitarsus, distal end crumpled, viewed from inferior side. F, K14498; distal end of tibia, prolateral view. G, K14565; patella of leg ?3, distal end to left, viewed from prolateral side. H, K14484; basitarsus; inferior prolateral view. I, K14480; basitarsus; prolateral view. J, K14526; distal portion of telotarsus with superior part of distal margin missing, lateral view. K, K14506 metasomal segment, anterior margin missing, superior lateral view. L, K14576 metasomal segment, superior view. M, K15475; vesicle and aculeus, the folded tip of the aculeus has been restored to its original position in the drawing. Abbreviations and conventions are given in 'Methods' in the text.

although too little well-preserved material (e.g. Pl. 2, fig. 13) has been recovered to enable a complete reconstruction.

Chelicerae are known only from dispersed cuticle remains. Superiorly the fixed finger bears a large compound tooth consisting of basal and median cusps, a subdistal tooth, and a large distal tooth. Inferior dentition consists of a row of five subequal teeth (Pl. 2, fig. 11; Pl. 6, fig. 6; Text-fig. 4E). The moveable finger has a superior row of five teeth which increase in size distally. The inferior dentition consists of the large distal tooth and an inferior row of approximately twelve small accessory teeth (Pl. 2, fig. 10; Pl. 6, fig. 4).

The pedipalp femur is known from only a few poorly-preserved fragments, but several well-preserved



TEXT-FIG. 6. *Cryptoscorpius americanus* gen. et sp. nov. Explanatory drawings for specimens illustrated in Plate 4. All specimens from Lone Star Lake, Kansas (Stephanian B), see Appendix for details of locality and horizon, and Plate 4 for scale. A, K14413; anterior portion of an adult carapace with both median eyes and left lateral eye group, anterior doublure reaches approximately the level of the tear between the two fragments. B, K14081; laterally compressed carapace, viewed from right side. C, K14080; carapace, left side folded under. D, K14097; dorsal surface of mesosomal tergite 7. E, K14095 ventral surface of metasomal segment with inferior and inferior lateral carinae. F, K14411; fragment of ventral surface of metasomal segment. G, K14099; right side of metasomal segment viewed from dorsal side, dorsal and inferior lateral carinae superimposed. H, K14410; fragment of right side of metasomal segment with strong dorsal carina, posterior end to right, viewed from dorsal side. I, K14096; dorso-ventrally flattened metasomal segment, viewed from dorsal side, part of anterior margin missing. Abbreviations and conventions are given in 'Methods' in the text.

examples of the patella have been recovered (e.g. Pl. 2, figs 6–7). In the original state the pedipalp patella was strongly carinate, each carina being marked by a diffuse row of larger than average tubercles. The precise number of carinae cannot be established in the flattened fossil material, but at least seven were present. Two internal carinae bear particularly large tubercles, each carrying a single setal follicle (Pl. 2, fig. 6). Only two trichobothria are present, and these are identified as eb and et (Text-fig. 4C, F).

The pedipalp manus is approximately half the length of the fixed finger. A row of tubercles marks the dorsal carina, but if other carinae were originally present they cannot be discerned in the fossil specimens. On the external face of the manus there is a large tubercular structure lying just proximally to the eb trichobothrium.

By analogy with similar structures in Recent bothrurids (Maury 1975), it is possible that this is a secondary sexual structure, although it is present in all of the larger manus fragments located so far, which suggests that they were present in both sexes and in sub-adult individuals. Specimens K14490 (Pl. 2, fig. 2; Text-fig. 4A–B), the distal end of a manus, has a trichobothrial distribution similar to that of *Palaeopisthacanthus*. The distribution in proximal regions of the manus is demonstrated by an adult specimen (K14461) although the cuticle is badly crumpled and K14416 was recovered from the same maceration residue as a large free finger (Pl. 2, fig. 5) and may be derived from the same individual. Dentition of the fingers consists of seven slightly oblique, but non-imbricated, primary sub-rows. The basal denticle of each sub-row forms a large tooth and there is a smaller inner accessory denticle on the proximal side of each one. Two large setal follicles are located proximally to the denticle pairs (Pl. 7, fig. 5). Each primary sub-row contains twelve to sixteen denticles.

Walking legs. Femora of walking legs 1–4 are ornamented with superior, inferior, and inferior prolateral carinae. In large specimens these are marked by rows of larger tubercles (Pl. 3, fig. 1; Text-fig. 5A), but the inferior prolateral may not be distinguishable in early instars (Pl. 3, fig. 2). Additional carinae may have been present in life but cannot be detected in the material available. Patellae have a single inferior carina (Pl. 3, fig. 3). In large specimens there is a row of tubercles along the inferior distal margin of the podomere prolaterally. The ornament of fine tubercles is present only on the adaxial surface. Tibiae bear a row of spinules in the distal two-thirds of the inferior surface (Pl. 3, fig. 4; Text-fig. 5D). Distally a second row of spinules is present in large specimens. Small spinules also occur around the prolateral distal margin (Pl. 3, fig. 7; Text-fig. 5F). In one specimen (K14496) from leg 3 or 4, a single tibial spur is present. Basitarsila are ornamented by four rows of fixed spinules. There are two rows located on the inferior surface, a prominent row on the prolateral surface, and a much weaker row on the retrolateral surface (Pl. 3, figs 5, 8–9; Text-fig. 5E, H–I). K14573 has cuticle more heavily ornamented with fine tubercles than other baritarsila of similar size, and the spinules are poorly developed. This may indicate that another species is present, but until further material is found this podomere is included in *C. elegans*, particularly as it exhibits no additional characters of phylogenetic significance. One specimen has been tentatively identified as a telotarsus. This consists of the distal end only of a podomere from a large individual, as indicated by the cuticle thickness and strong ornament, and bears an inferior row of fixed cuticular thorns. A row of tiny spinules is present along the distal margin in the inferior prolateral portion (Pl. 3, fig. 10; Text-fig. 5J). The superior portion of the distal margin is missing, but from the parts preserved it is evident that lateral lobes were not developed.

Discussion. Kjellesvig-Waering (1986, p. 236) diagnosed *Compsoscorpius* simply by reference to its palaeopisthacanthid affinities and the rounded carapace anterior margin. The anterior margin is entire only in the holotype, and its rounded appearance in Kjellesvig-Waering's (1986, text-fig. 105) drawing is illusory, because the carapace is slightly distorted within the nodule.

Genus CRYPTOSCORPIUS gen. nov.

Derivation of name. *Cryptos* (Gr.) – hidden, combined with *skorpios* (Gr.) – a scorpion.

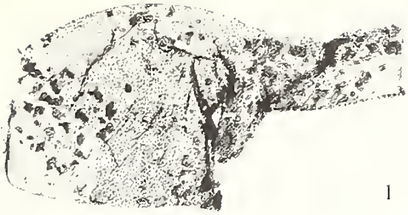
Type species. *Cryptoscorpius americanus* gen. et sp. nov.

EXPLANATION OF PLATE 5

Fig 1. *Corniops mapesii* gen. et sp. nov. K14082; holotype, pedipalp manus and part of fixed finger; see Text-figure 5A for explanation; Lone Star Lake, Kansas, Upper Carboniferous (Stephanian B); ×32.

Figs 2–3, 5–10. *Cryptoscorpius americanus* gen. et sp. nov. All specimens from Lone Star Lake, Kansas, Upper Carboniferous (Stephanian B). 2, K14083*a*; holotype, pedipalp manus and fixed finger; see Text-figure 5B for explanation; ×32. 3, K14404; juvenile basitarus, proximal end missing; see Text-figure 5C for explanation; ×39. 5, K14085*b*; partial pedipalp finger; ×26. 6, K14083*b*; paratype, partial pedipalp manus and fixed finger; see Text figure 6F for explanation; ×32. 7, K14415; femur of walking leg ?3; ×26. 8, K14088; walking leg 4; ×26. 10, K14084*a*; juvenile trochanter and femur of walking leg ?4; see Text-figure 7E for explanation; ×32.

Fig. 4. *Palaeopithacanthus vogelandurdeni* sp. nov. K14086; holotype, distal end of pedipalp manus and fixed finger; see Text-Figure 6D for explanation; ×32.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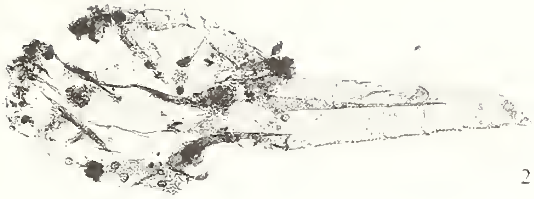
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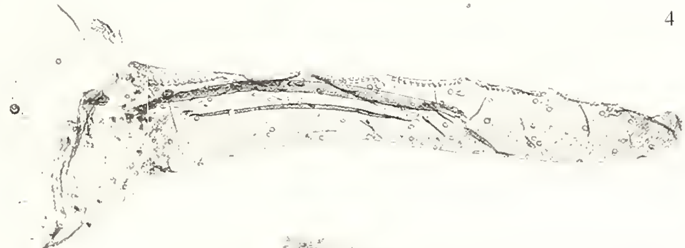
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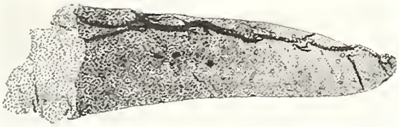
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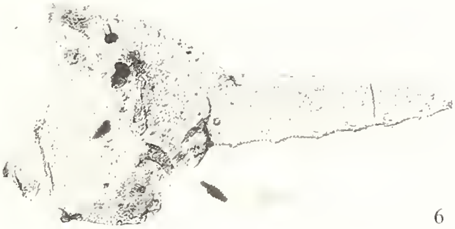
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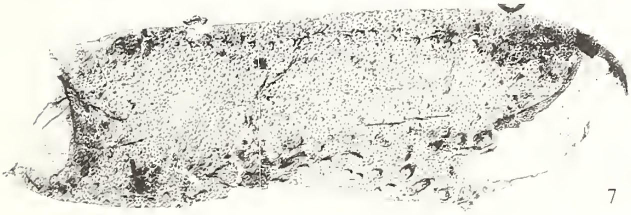
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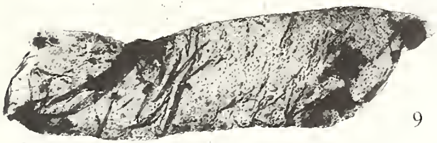
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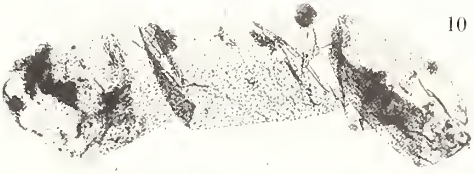
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JERAM, *Corniops*, *Cryptoscorpius*, *Palaeopithacanthus*

Diagnosis. Palaeopisthacanthid with pedipalp fingers approximately equal in length to manus. Seven primary sub-rows on pedipalp fingers with nine or ten denticles in each.

Cryptoscorpius americanus sp. nov.

Plate 2, figures 8–9; Pl. 4; Plate 5, figures 2–3, 5–10; Plate 6, figures 1–3; Plate 7, figures 3–4, 7; Text-figures 4D; 6; 7B–C, E–F, H, I; 8A, C–D.

Derivation of name. americanus, referring to the geographical province.

Holotype. Pedipalp manus and fixed finger K14083*a*, from cuticular shale immediately overlying the Lower Williamsburg Coal Member of the Douglas Shale Formation, at Lone Star Lake Spillway, Douglas County, Kansas, USA.

Paratypes. K14083*b*, incomplete pedipalp manus and fixed finger. K14079, incomplete juvenile scorpion. K14080 and K14081, sub-adult carapaces. All from same locality and horizon as the holotype. Other material is listed in Appendix 1.

Diagnosis. As for genus.

Description. The most complete specimen recovered is a small juvenile in which the prosoma and part of the mesosoma is preserved (Pl. 6, fig. 1; Text-fig. 8A). The specimen is distorted and partly obscured by insoluble opaque organic matter, but nevertheless it reveals several characters which confirm the position of this species in the Palaeopisthacanthidae. In particular, the coxae of walking-legs 3 and 4 both abut the sternum which is sub-pentagonal (in its undistorted state) and slightly longer than broad. The coxal apophyses of walking-legs 1 and 2 (left) have been displaced anteriorly, rotated, and overturned, but are clearly of the palaeopisthacanthid-type, with both apophyses of approximately equal length and breadth. Lateral eye nodes could not be detected on the very thin juvenile cuticle. The first mesosomal sternite, underlying tergite 1 in Text-figure 8A, is very short compared with those of the Recent scorpions, supporting Kjellesvig-Waering's (1986) contention that an anterior sternite underlies the pectines in the holotype of *Palaeopisthacanthus schucherti*, and that four sternites are present in the palaeopisthacanthids. Characters of greater taxonomic use are revealed by the more mature, but fragmentary, material described below.

Carapace. Two nearly complete sub-adult carapaces and one partial adult carapace have been recovered, in addition to numerous fragments attributable to this sclerite. The carapace outline is similar to those of *Palaeopisthacanthus* and *Compsoscorpius*, and there is no evidence of an anterior glossate process. The median eyes are large, and located posteriorly to the lateral eye nodes. Lateral margins are marked by a longitudinal ridge similar to the transverse ridge characteristic of scorpion tergites, and there are rows of larger tubercles along the anterior and posterior carapace margins (Pl. 4, figs 1–3). The lateral eye groups are located on raised

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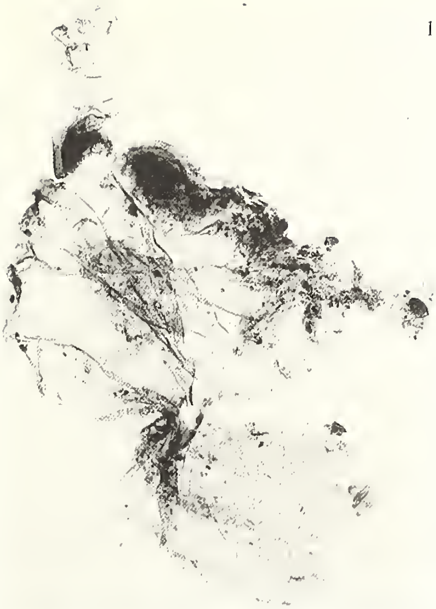
EXPLANATION OF PLATE 6

Figs 1–3. *Cryptoscorpius americanus* gen. et sp. nov. Lone Star Lake, Kansas; Upper Carboniferous (Stephanian B). 1, K14079; paratype, partial juvenile specimen; see Text-figure 7A for explanation; × 32. 2, K14413; left lateral eye group; see Text-figure 7C for explanation; NDIC photography; × 130. 3, K14081; right lateral eye group; see Text-figure 7D for explanation; NDIC photography; × 257.

Figs 4–7. *Compsoscorpius elegans* Petrunkevitch, 1949. See Appendix for localities. All specimens Upper Carboniferous (Westphalian B). 4, K14564; detail of cheliceral free finger dentition, viewed from exterior side; NDIC photography; × 130. 5, K14546; detail of cheliceral fixed finger dentition viewed from internal side; NDIC photography; × 130. 6, K14563; inner surface of vesicle cuticle showing two sunken pores; NDIC photography; × 257. 7, K14488; detail of femur cuticle with two probable arachnid tarsila preserved within lumen of podomere; NDIC photography; × 130.

Fig. 8. *Gymnoscorpius mutillidigitus* gen. et sp. nov. K14575; detail of vesicle cuticle with characteristic form of microseta (top left), and abundant mite setae preserved in lumen of sclerite; Lowther North Opencast Site, Barnsley Seam (Westphalian B); NDIC photography; × 257.



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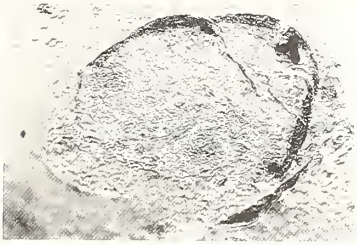

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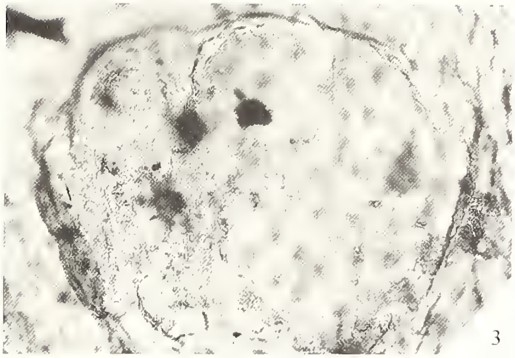

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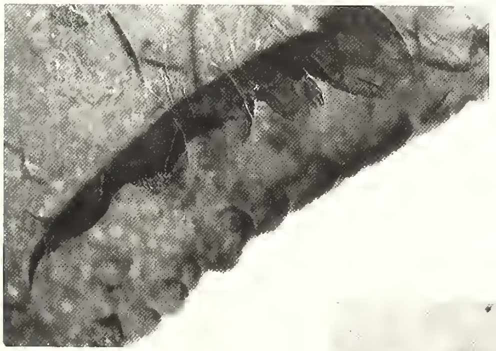

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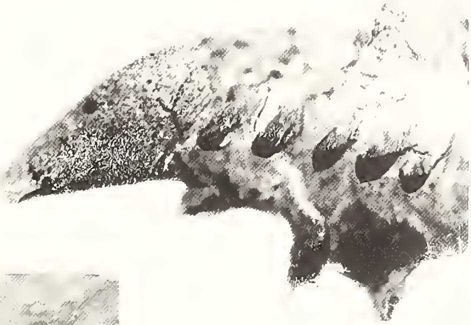

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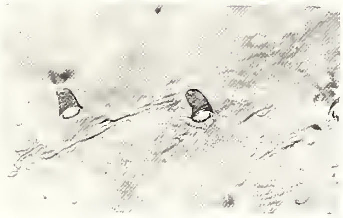

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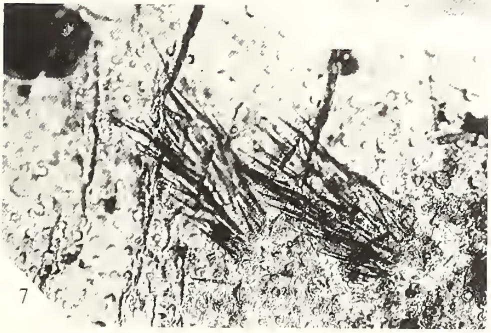

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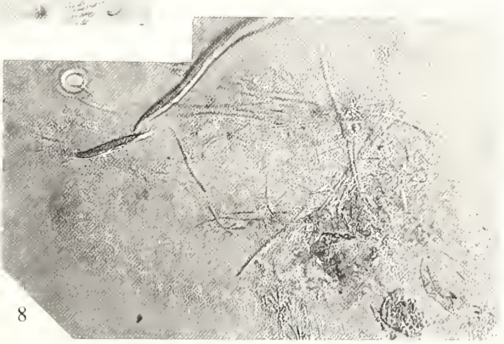

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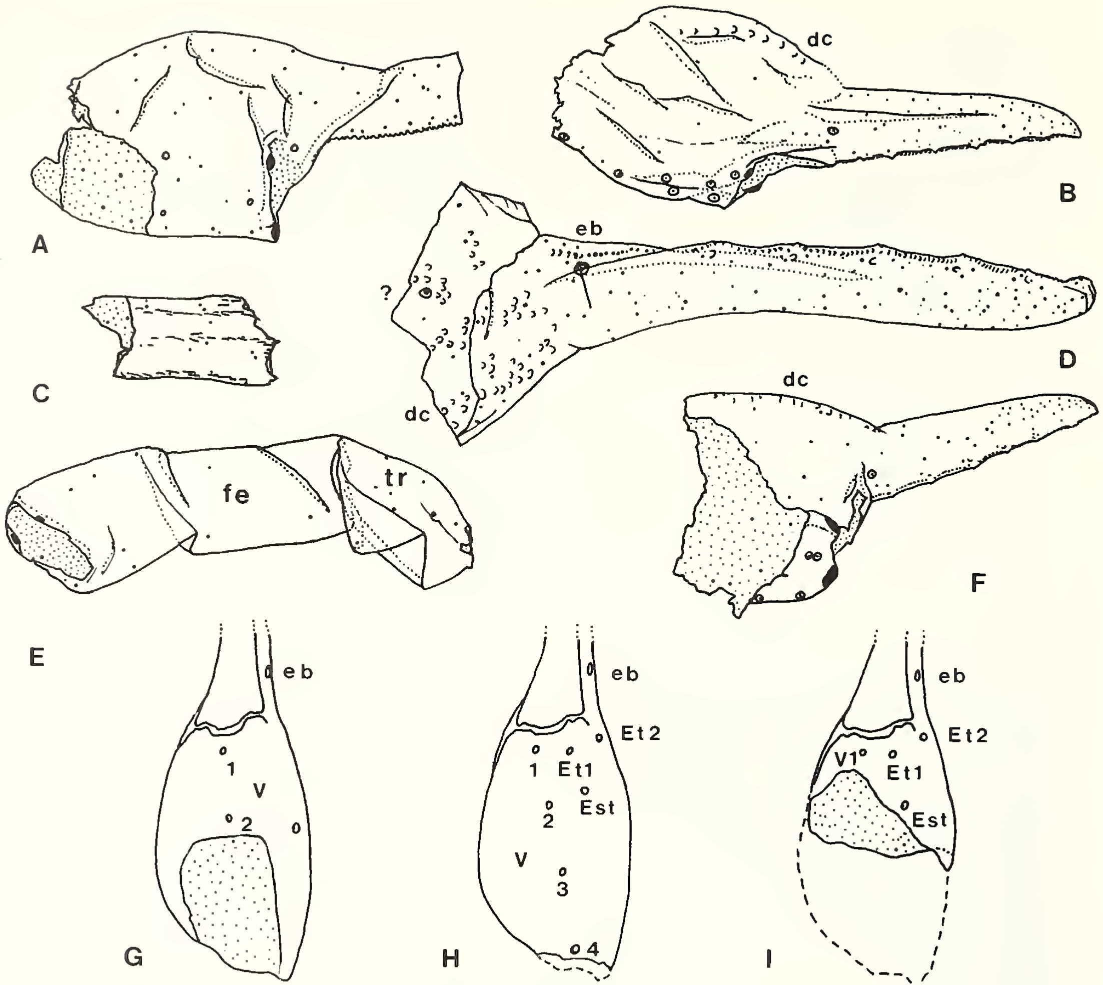
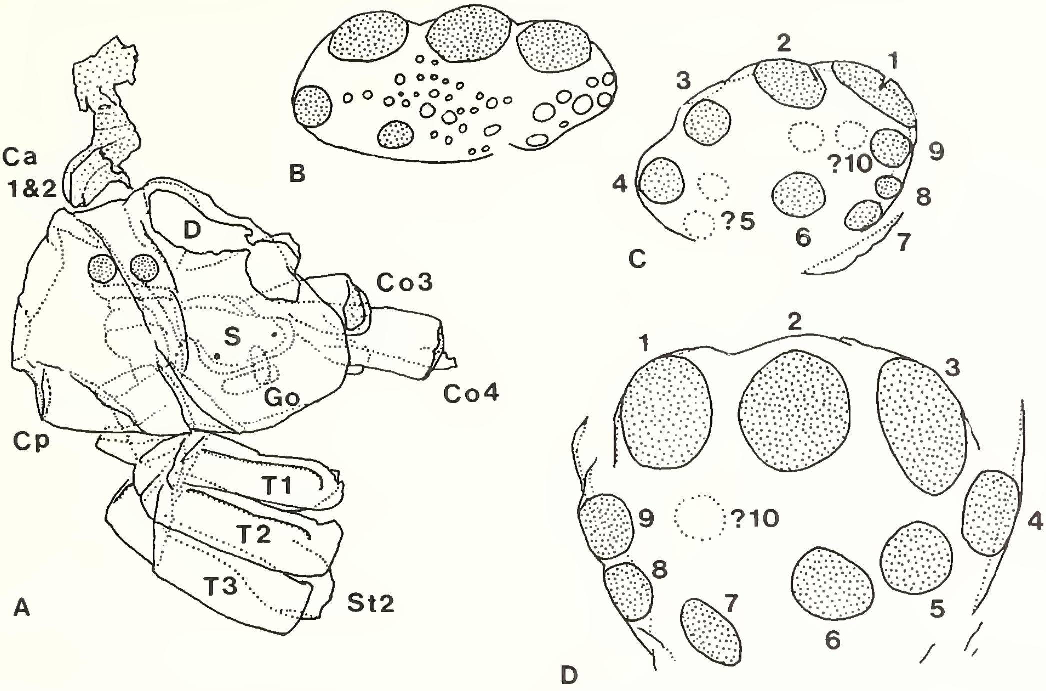
JERAM, *Cryptoscorpius*, *Compsoscorpius*, *Gymnoscorpius*



TEXT-FIG. 7. *Corniops mapesii* gen. et sp. nov. (A, G); *Cryptoscorpius americanus* gen. et sp. nov. (B–C, E–F, H–I); and *Palaeopithacanthus vogelandurdeni* sp. nov. (D). Explanatory drawings for specimens illustrated in Plate 5. All specimens from Lone Star Lake, Kansas (Stephanian B). See Plate 5 for scale. A, K14082; pedipalp manus and part of fixed finger, bothria not designated, see G for explanation; B, K14083*a*, holotype; pedipalp manus and fixed finger, proximal margin missing. C, K14404; distal end of basitarsus, part of distal margin missing, viewed from inferior side. D, K14086, holotype; distal portion of pedipalp manus and fixed finger, superior surface bottom of drawing, viewed from external side. E, K14084*a*; trochanter and femur of leg ?4; viewed from axial side, distal end on left. F, K14083*b*; paratype, distal end of pedipalp manus and fixed finger, viewed from internal side. G, reconstruction of trichobothrial distribution in K14082; (see Fig. 7A), viewed from ventral side. H, reconstruction of trichobothrial distribution in K14083*a* (see Fig. 7B), viewed from ventral side. I, reconstruction of trichobothrial distribution in K14083*b*; (see Fig. 7F), viewed from ventral side. Abbreviations and conventions are given in the section 'Methods' in the text.

nodes. Ocelli are most evident in the adult specimen (Pl. 6, fig. 2; Text-fig. 8C), but can also be recognized in the other specimens (Pl. 6, fig. 3; Text-fig. 8D). Three major ocelli are present on the external side of the node and up to seven minor ocelli can also be distinguished, although it is not possible in every case to be certain that the features recognized are ocelli rather than tubercles on the eye node. Employing NDIC at high magnification was useful because the cuticle surface of ocelli is much smoother than that of background cuticle,



TEXT-FIG. 8. *Cryptoscorpius americanus* gen. et sp. nov. (A, C–D); *Lychas* sp. (Recent; Buthidae) (B). Explanatory drawings for some specimens illustrated in Plate 6. A, K14079, paratype; partial juvenile specimen viewed from dorsal side, × 32. B, left lateral eye group of Recent buthid scorpion (*Lychas* sp.) showing major and minor ocelli, stippled areas are ocelli, open areas are tubercles on eye node; anterior to right; × 50. C, left lateral eye group of specimen K14413 (see Plate 6, figure 2). Stippled areas are ocelli, broken circles indicate possible ocelli which are numbered anticlockwise from the large anterior ocellus; ocellus no. 5 could not be located with certainty, although there are two patches of cuticle which might represent it; × 130. D, right lateral eye group of specimen K14081 (see Plate 6, figure 3). Drawing conventions as above. Anterior is to left, so numbering of ocelli is clockwise in this specimen; × 260. (In C and D the locations of ocelli were determined by careful use of NDIC microscopy which produces a very small depth of focus, so not all ocelli are clearly visible in the figures on Plate 6). Abbreviations and conventions are given in 'Methods' in the text.

including tubercles, so in certain planes of focus refraction by the ocellar cuticle surface is less than from surrounding cuticle, and the ocelli appear as semi-transparent patches on the cuticle (Pl. 6, fig. 3).

Tergites. Mesosomal tergites 1–6 do not differ in any significant respect from those of other palaeopisthacanthids. However, in large individuals the dorsal surface of tergite 7 bears four strong carinae, each marked by a row of large tubercles. These are present in the posterior half of tergite 7, and anteriorly are linked by a transverse row of tubercles (Pl. 4, fig. 4; Text-fig. 6D). Tergites 1–6 lack carinae.

Sternites. In addition to the incomplete juvenile described above, only a few specimens of sternites have been found, and these are not significantly different from other palaeopisthacanthid sternites.

Metasoma. The caudal segments are similar to those of *Palaeopisthacanthus* and *Compsoscorpius*. Carinae, particularly the dorsal pair, are more prominent, and as in *Compsoscorpius*, an anterior transverse ridge is present around the circumference of each segment (Pl. 4, figs 5–9; Text-figs 6E–I). The vesicle and aculeus are unknown.

Prosomal appendages. The coxosternal arrangement of the species is seen only in the juvenile specimen, K14079, although isolated fragments of coxae, and one complete specimen of coxa 3, have been recovered. Pectines are represented by a fragment associated with two sternites (K14405). This consists of a partial lamina with 14 teeth, although judging by the portion preserved, up to 20 teeth may have originally been present on each comb. Only a small number of well-preserved palaeopisthacanthid podomeres have been recovered from the Lone Star Lake locality, and so it is not possible to be certain which of these belong to *Cryptoscorpius* or to one of the other taxa in the assemblage. A large (?adult) femur (K14415; Pl. 5, fig. 7) has cuticle with a thickness and intensity of fine tubercles similar to that of the carapace specimen K14413, so it can reasonably be attributed to *Cryptoscorpius*. Almost all of the cuticle ornament is on the adaxial surface of the femur. There are strong inferior, inferior prolateral, and superior carinae, each marked by larger tubercles. The length: breadth ratio of this podomere suggests that it is from walking-leg 3. A second femur (K14084b, Pl. 5, fig. 9) is probably from leg 4. It has thicker, and darker, cuticle than other palaeopisthacanthid podomeres of this size, and in addition to the three carinae present on the specimen cited above, it has a superior prolateral carina. It is approximately the same size as a third specimen, K14084*a* (Pl. 5, fig. 10; Text-fig. 7E), which appears to lack carinae, and is also unusual in having very little cuticle ornament on the superior surface. K14084*a* could well be a juvenile of the same species as K14415, but K14084*b* may be derived from a different species (e.g. *Corniops mapesii* gen. et sp. nov.). However, until more material is available, all podomeres in the assemblage are provisionally attributed to *C. americanus*. A single juvenile patella (Pl. 5, fig. 8) has the rudiments of an inferior carina, and a proximal fragment of the tibia is still articulated with this specimen. Only one example of the basitarsus is known (Pl. 5, fig. 3; Text-fig. 7C). Like *Compsoscorpius*, this has four rows of long spinules; a strong inferior prolateral, two inferior, and a weak inferior retrolateral row. The telotarsus, apotele, and claws are unknown.

ORTHOSTERNI *incertae sedis*

Genus CORNIOPS gen. nov.

Derivation of name. An anagram of 'scorpion'.

Type species. *Corniops mapesii* gen. et sp. nov.

Diagnosis. Dentition of pedipalp finger consisting of single straight file of denticles. No accessory denticles present. Bothria of simple type, without deep cup. Lacking well developed superior carina on pedipalp manus.

Discussion. The cuticle of this genus is of the palaeopisthacanthid-type, but the distinctive pedipalp dentition and bothrial structure exclude it from the Palaeopisthacanthidae. Until further material is recognized the genus can be provisionally regarded as Orthosterni *incertae sedis*, since there are no other derived characters in the only available specimen which are shared with any fossil scorpion.

Corniops mapesii sp. nov.

Plate 5, figure 1; Plate 7, figure 8; Text-figure 7A, G.

Derivation of name. This species is named for Gene Mapes who recognized the presence of scorpions at the Lone Star Lake locality.

EXPLANATION OF PLATE 7

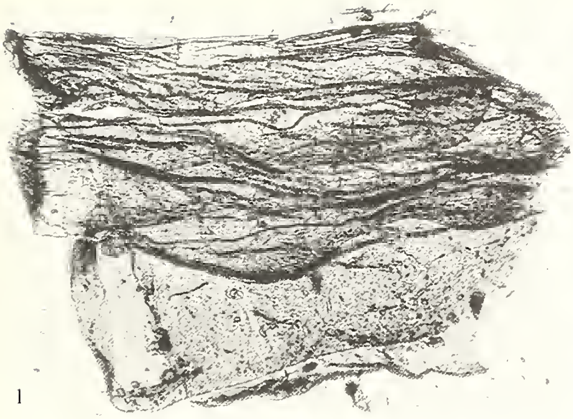
Figs 1, 5. *Compsoscorpius elegans* Petrunkevitch, 1949. Swillington Brickpit, Yorkshire; Upper Carboniferous (Westphalian B). 1, K14473; partial juvenile mesosoma with three crumpled sternites, and tergites 5–7; × 43. 5, K14490; detail of pedipalp finger dentition, distal end to right; NDIC photography; × 130.

Fig. 2. *Gymnoscorpius mutillidigitus* gen. et sp. nov. K14479; holotype, detail of pedipalp dentition, distal end to left; NDIC photography; × 257.

Figs 3–4, 7. *Cryptoscorpius americanus* gen. et sp. nov. Lone Star Lake, Kansas; Upper Carboniferous (Stephanian B). 3, K14083*b*; paratype, detail of pedipalp dentition, distal end to left; NDIC photography; × 130. 4, K14083*a*; holotype, detail of pedipalp dentition, distal end to left; NDIC photography; × 130. 7, K14416; detail of bothrium on fragment of an adult pedipalp ?manus. Note spiralling cristae within cup of bothrium; NDIC photography; × 257.

Fig. 8. *Corniops mapesii* gen. et sp. nov. K14082; holotype, detail of pedipalp manus viewed from inferio-exterior side; large follicles are probable bothria; dark material is adherent plant cuticle; Lone Star Lake, Kansas; Upper Carboniferous (Stephanian B); NDIC photography; × 105.

PLATE 7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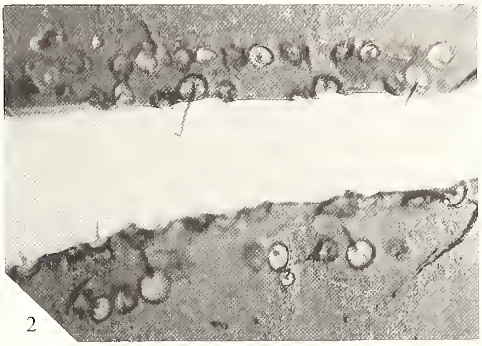
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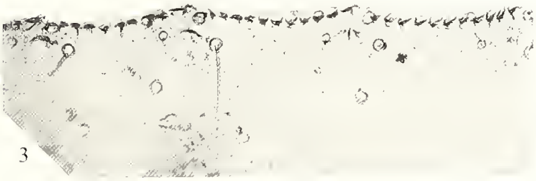
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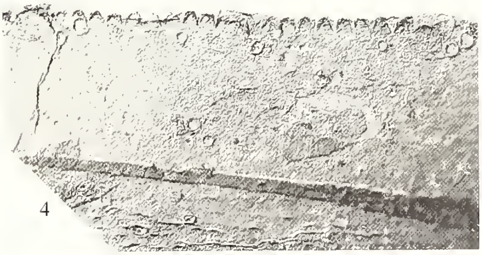
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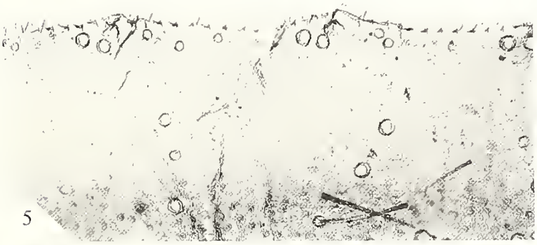
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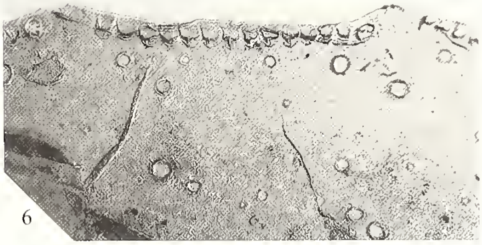
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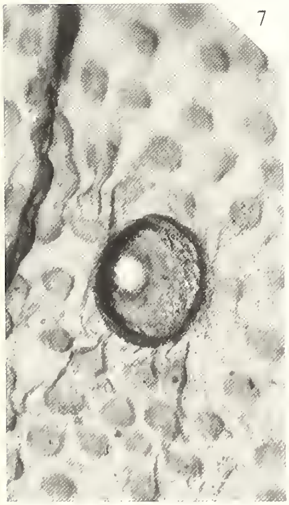
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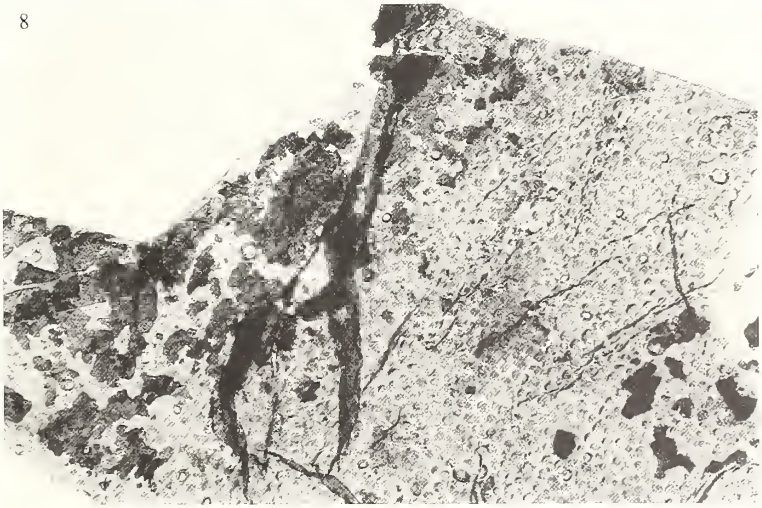
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JERAM, *Compsoscorpius. Gymnoscorpius. Cryptoscorpius, Corniops*

Holotype. K14082; the only known specimen, a partial pedipalp manus with proximal portion of the fixed finger. From cuticular shale immediately overlying the Lower Williamsburg Coal, at Lone Star Lake Spillway, Douglas County, Kansas.

Diagnosis. As for genus.

Description. The cuticle is thicker and darker in colour than palaeopisthacanthid pedipalps of a similar size, and the cuticle ornament is bolder and very evenly distributed over the manus. Most setal follicles are small, but a few larger examples are present on the inferior and external surfaces (Pl. 7, fig. 8), and given their positions it is likely that they housed trichobothria. However, their structure is similar to that of normal setal follicles, and no cup-shaped bothria characteristic of palaeopisthacanthids and Recent scorpions are present. Two ventral trichobothria and an eb trichobothrium were probably present. A fourth bothrium lies on the external surface level with V_2. Unfortunately the proximal part of the manus ventral surface is missing, so it is unknown if any further ventral or basal trichobothria were present originally.

Only a proximal portion of the fixed finger is present, but sufficient is preserved to establish that the dentition consists of a single continuous primary row of denticles, with no accessory denticles present.

NEOSCORPIONINA *incertae sedis*

Genus GYMNOSCORPIUS gen. nov.

Derivation of name. From *gymnos* (Gr.) – naked, and *skorpios* (Gr.) – a scorpion, referring to the cuticle of this genus which lacks macrosetae and is unornamented.

Type species. Gymnoscorpius mutillidigitus gen. et sp. nov.

Diagnosis. Cuticle lacking macrosetae. Pedipalp fingers equal in length to hand, with poorly defined denticles of palaeostern-type alternating with setal follicles in primary row. Accessory denticles present. Cuticle surface smooth and entirely lacking ornament.

Discussion. This genus cannot be placed in any existing scorpion family, and since the coxosternal configuration, carapace, and sternites, are all unknown its systematic position is problematic. The cuticle characteristics are similar to palaeosterns, as is the form of the pedipalp denticles. Setal characteristics and lack of ornament are unique. Short pedipalp fingers are known in *Garnettius* (the systematic position of which is also problematic) and the Orthosterni. Sunken ducts present in *Gymnoscorpius* have only otherwise been observed in palaeopisthacanthids. For the present therefore, *Gymnoscorpius* is provisionally assigned to the Neoscorpionina.

Gymnoscorpius mutillidigitus sp. nov.

Plate 3, figures 11–16; Plate 6, figure 8; Plate 7, figure 2; Text-figure 5K–M.

Derivation of name. From *mutilatus* (L.) – cut short, combined with *digitus* (L.) – a finger, referring to the short pedipalp fingers of this species.

Holotype. K14479, a complete pedipalp chela with fixed and free fingers, from bed 20F at Swillington Brickpit, near Leeds, Yorkshire.

Paratypes. K14578, an incomplete pedipalp manus and fixed finger from the Barnsley Seam at Lowther North Opencast Mine, Yorkshire. K14491, large pedipalp patella, and K14506, caudal segment, from bed 20F at Swillington Brickpit. K14476, partial femur, from bed 18 at Swillington Brickpit. K14576, caudal segment, and K14575, vesicle, both from same maceration residue, Barnsley Seam, Lowther North Opencast Mine. K14525, cuticle fragment, Wigan Five Foot Coal, Pemberton Opencast Mine, near Wigan, Lancashire.

Diagnosis. As for genus.

Description. Even small fragments of the cuticle are very distinctive. When viewed in transmitted light it has a particularly bright and refractive appearance compared with other fossil scorpion cuticles, and it is smooth, lacking all forms of cuticle surface sculpture or ornament. The openings of cuticular ducts are easily visible, and on the postabdominal segments most take the form of sunken pores (see above). Macrosetae are absent, but sparse microsetae are scattered over the surface and are most abundant on the pedipalp fingers. Prominent clusters of slit sensillae occur near the distal articulations of the pedipalp patella (Pl. 3, fig. 11).

The pedipalp manus is very short, as are the fingers which are approximately the same length as the manus. No trichobothria are present. Pedipalp dentition consists of a single straight primary denticle row in which weakly developed denticles of palaeostern-type alternate with setal follicles. Accessory denticles are present in linear clusters along the fingers (Pl. 3, fig. 13; Pl. 7, fig. 2).

Caudal segments are short and bulbous in shape, lacking lateral and ventral carinae. A pair of dorsal carinae is present, ornamented by a single large tubercle at the anterior end of each carina (Pl. 3, figs 14–15; Text-fig. 5K–L). The vesicle was apparently very bulbous in life, but specimen K14575 is too crushed and complexly folded to reconstruct its shape accurately. The aculeus is short (Pl. 3, fig. 16; Text-fig. 5M). All other parts of this species are unknown.

Remarks. *Gymnoscorpius* is very rare, with only eight specimens recognized from among nearly 12000 Upper Carboniferous scorpion cuticles examined. The largest specimens (e.g. K14578) are derived from individuals with an estimated body length of no more than 30 mm.

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APPENDIX 1

List of material used in study

Belum No.	Brief description	Illustration	Locality
Palaeopisthacanthus schucherti			
K14420	coxa 3, 4 + trochanter	—	7
K14421	postabdominal segment	—	7
K14422	coxal apophyses	—	7
K14423	tergite + sternite	—	7
K14425	tergite	—	7
K14426	pedipalp patella	—	7
K14427	pedipalp femur	—	7
Compsoscorpius elegans			
K14428	pedipalp finger	Pl. 2, fig. 3	1
K14429	tergite	—	5 (18)
K14430	tergite	—	5 (18)
K14432	pedipalp finger	Pl. 2, fig. 5	5 (18)
K14433	postabdominal segment	Pl. 1, fig. 4; Text-fig. 3C	5 (18)
K14434	trochanter	—	5 (18)
K14435	femur	—	5 (18)
K14436	pedipalp manus + fixed finger	—	5 (18)
K14437	tergite	—	5 (18)
K14438	tergite	—	5 (18)
K14440	postabdominal segment	—	5 (18)
K14442	tergite	—	5 (18)
K14444	trochanter	—	5 (18)
K14445	femur	—	5 (18)
K14446	patella	—	5 (18)
K14448	coxa	—	5 (18)
K14449	tergite	—	5 (18)
K14450	tergite	—	5 (18)
K14451	pedipalp manus + fixed finger	—	5 (18)
K14452	trochanter	—	5 (13)
K14454	tergite	—	5 (18)
K14455	tergite	—	5 (18)
K14457	carapace	—	5 (18)
K14458	femur	Pl. 3, fig. 2; Text-fig. 5B	5 (18)
K14460	pedipalp patella	Pl. 2, fig. 6; Text-fig. 4F	5 (18)
K14464	femur	—	5 (18)
K14470	tergite	—	5 (13)
K14471	pedipalp patella	—	5 (13)
K14472	sternite	Pl. 1, fig. 5; Text-fig. 3F	5 (13)

APPENDIX 1 (*cont.*)

Belum No.	Brief description	Illustration	Locality
K14473	partial mesosoma	Pl. 7, fig. 1	5 (13)
K14474	metasomal segment	—	5 (13)
K14475	partial mesosoma	Pl. 1, figs. 1, 3; Text-fig. 3A	5 (13)
K14480	basitarsus	Pl. 3, fig. 9; Text-fig. 5I	5 (20F)
K14481	metasomal segment	Pl. 1, fig. 7; Text-fig. 3B	5 (20F)
K14484	basitarsus	Pl. 3, fig. 5; Text-fig. 5H	5 (20F)
K14485	pedipalp finger	Pl. 2, fig. 1	5 (20F)
K14488	femur	Pl. 3, fig. 1; Pl. 6, fig. 7; Text-fig. 5A	5 (20F)
K14490	pedipalp manus + finger	Pl. 2, fig. 2; Pl. 7, fig. 5; Text-fig. 4A	5 (20F)
K14494	vesicle	—	5 (20F)
K14496	tibia + spur	Pl. 3, fig. 3; Text-fig. 5D	5 (20F)
K14498	tibia	Pl. 3, fig. 7; Text-fig. 5F	5 (20F)
K14499	coxa 2	Pl. 2, fig. 13	5 (20F)
K14500	pedipalp finger	Pl. 2, fig. 4	5 (20F)
K14503	patella	—	5 (20F)
K14504	tergite	Pl. 1, fig. 2	5 (20F)
K14507	femur	—	5 (20F)
K14509	pedipalp ?femur	—	5 (20F)
K14510	basitarsus	Pl. 3, fig. 8; Text-fig. 5E	5 (20F)
K14517	metasomal segment	Pl. 1, fig. 9; Text-fig. 3G	4
K14518	pedipalp	—	4
K14519	femur	—	4
K14521	femur	—	4
K14522	femur	—	4
K14523	?pedipalp trochanter	—	4
K14524	femur	—	4
K14526	telotarsus	Pl. 3, fig. 10; Text-fig. 5J	4
K14527	carapace (fragment)	—	4
K14528	coxal apophyses	—	4
K14529	metasomal segment	—	4
K14530	tergite	—	4
K14531	carapace	—	4
K14532	tergite	—	4
K14533	sternite	Pl. 1, fig. 6; Text-fig. 3D	4
K14535	sternite	—	4
K14537	tergite	—	4
K14539	tergite 7	—	4
K14540	tergite 7	—	4
K14541	sternite	—	4
K14543b	chelicera	—	4
K14545	pedipalp finger	—	4
K14546	chelicera	Pl. 2, fig. 11; Pl. 6, fig. 5; Text-fig. 4E	4
K14547	pedipalp finger	—	4
K14548	femur	—	4
K14549	patella	—	4
K14550	basitarsus	—	4
K14551	vesicle + aculeus	—	5 (20F)
K14552	pedipalp finger	—	6b
K14553	pedipalp manus + finger	—	6b
K14556	pedipalp finger	—	6a
K14557	pedipalp finger	—	6a
K14561	juvenile pedipalp femur	—	6a

APPENDIX 1 (*cont.*)

Belum No.	Brief description	Illustration	Locality
K14562	pedipalp patella	—	6b
K14563	vesicle + aculeus	Pl. 6, fig. 6	6a
K14564	cheliceral free finger	Pl. 2, fig. 10; Pl. 6, fig. 4	6a
K14565	patella	Pl. 3, fig. 3; Text-fig. 5G	6a
K14566	pedipalp patella	Pl. 2, fig. 7; Text-fig. 4C	6a
K14570	metasomal segment	Pl. 1, fig. 8; Text-fig. 3E	6a
K14571	vesicle + aculeus	Pl. 2, fig. 12	6a
K14573	basitarsus	Pl. 3, fig. 6; Text-fig. 5C	6b
K14579	pedipalp finger + pectine	—	6a
K14580	pedipalp finger	—	6a
K17036	trochanter	—	2
K17036	trochanter	—	2
K17037	?patella	—	2
K17038	femur	—	2
K17039	femur	—	2
K17040	metasomal segment	—	2
K17041	cheliceral free finger	—	2
K17042	cuticle scraps	—	3
Cryptoscorpius americanus			
K14079	**paratype** partial juvenile	Pl. 6, fig. 1; Text-fig. 8A	8
K14080	**paratype** carapace	Pl. 4, fig. 3; Text-fig. 6C	8
K14081	**paratype** carapace	Pl. 4, fig. 2; Pl. 6, fig. 3; Text-figs 6B, 8D	8
K14083a	**holotype** pedipalp	Pl. 5, fig. 2; Pl. 7, fig. 4; Text-fig. 7B	8
K14083b	**paratype** pedipalp	Pl. 5, fig. 6; Pl. 7, fig. 3; Text-fig. 7F	8
K14084a	femur + trochanter	Pl. 5, fig. 10; Text-fig. 7E	8
K14084b	femur	Pl. 5, fig. 9	8
K14085a	pedipalp finger	—	8
K14085b	pedipalp finger	Pl. 5, fig. 5	8
K14087	partial mesosoma	—	8
K14088	patella + tibia	Pl. 5, fig. 8	8
K14090	femur	—	8
K14091	pedipalp finger	—	8
K14092	pedipalp finger	—	8
K14093	tergite	—	8
K14094	tergite	—	8
K14095	metasomal segment	Pl. 4, fig. 6; Text-fig. 6E	8
K14096	metasomal segment	Pl. 4, fig. 8; Text-fig. 6I	8
K14097	tergite 7	Pl. 4, fig. 4; Text-fig. 6D	8
K14098	coxa 3	Pl. 2, fig. 9	8
K14099	metasomal segment	Pl. 4, fig. 9; Text-fig. 6G	8
K14100	tergite 7	Pl. 4, fig. 4; Text-fig. 6D	8
K14401	pedipalp ?patella	—	8
K14402	pedipalp femur	Pl. 2, fig. 8; Text-fig. 4D	8
K14403	tergite	—	8
K14404	basitarsus	Pl. 5, fig. 3; Text-fig. 7C	8
K14405	partial mesosoma + pectine	—	8
K14406	tergite	—	8
K14407	tergite	—	8
K14408	tergite	—	8
K14409	tergite	—	8
K14410	metasomal segment	Pl. 4, fig. 5; Text-fig. 6H	8
K14411	metasomal segment	Pl. 4, fig. 7; Text-fig. 6F	8

APPENDIX 1 (*cont.*)

Belum No.	Brief description	Illustration	Locality
K14412	metasomal segment	—	8
K14413	carapace	Pl. 4, fig. 1; Pl. 6, fig. 2; Text-figs 6A, 8C	8
K14414	trochanter	—	8
K14415	femur	Pl. 5, fig. 7	8
K14416	pedipalp patella	Pl. 7, fig. 7	8
K14417	pedipalp ?patella	—	8
K14418	metasomal segment	—	8
K14419	?metasomal segment	—	8
K17048	pedipalp finger	—	8
K17049	tergite	—	8
K17050	metasomal segment	—	8

ARE CONCHIOLIN SHEETS IN CORBULID BIVALVES PRIMARILY DEFENSIVE?

by ELIZABETH M. HARPER

ABSTRACT. Conchiolin sheets in corbulid bivalves have long been considered to offer some defence against predation by boring gastropods. Vermeij argued that most defences are exaptions rather than adaptations, but it has never been demonstrated whether conchiolin sheets in corbulids evolved in response to predation pressure or as a fortuitous benefit of an otherwise selected character (e.g. to retard shell dissolution, to prevent crack propagation, or to assist with hermetic sealing). A three pronged investigation was undertaken to resolve this question: a survey of failure rate of gastropod boreholes in corbulids over geological time, a survey of the distribution of conchiolin sheets in Recent corbulids in relation to various selection pressures, and an investigation into the temporal appearance of the sheets by direct (microstructural) and indirect (inferred from morphology and taphonomy) means. It is concluded that well developed conchiolin sheets first appeared at a time coincidental with the first reported gastropod boreholes and that they evolved primarily in response to that threat. Possession of conchiolin sheets may then have further influenced corbulid evolution in allowing the assumption of gross valve discordance in post-Jurassic taxa.

GOULD and Vrba (1982) considered aptations (beneficial traits) and distinguished between *adaptations* (traits whose perceived benefit for a specified function or effect has been enhanced by natural selection) and *exaptations* (traits whose benefits to the owner are secondary or incidental to the primary function to which they are adapted). Given that many traits may be multifunctional (i.e. beneficial in a number of unrelated ways) these functions should be divisible into adaptations and exaptations. Vermeij (1982) believed most anti-predatory aptations to be exaptations.

Vermeij (1983) noted that the bivalved form of both bivalves and brachiopods is susceptible to damage, and that even non-lethal attacks will often be ultimately fatal because of their poor ability to repair marginal damage. It therefore follows that both must have been affected by the 'sudden' increase in predation pressure following the Mesozoic Marine Revolution (MMR) of Vermeij (1977, 1987) and are likely to display a number of defensive adaptations. For the bivalved molluscs a large number of defences have been described (Carter 1968; Ansell 1969; Vermeij 1987). Harper and Skelton (1993*a*) noted the desirability of testing to ascertain whether changes in morphology and life habit are truly defensive. Even so, although it may be possible to demonstrate experimentally that a specific trait confers a selective advantage against a given predator, it may be more problematic to show that it evolved directly in response to that threat and was thus an adaptation. For example, Logan (1974) considered the functional morphology of the spines of the bivalve *Spondylus americanus*. He discusses six functions for these spines, all of which are demonstrable. Only two of these may be described as directly defensive (protection of the gape and promoting the growth of camouflaging algae), the remainder being concerned with anchorage, discouraging epibionts and providing support for sensory outposts.

In order to distinguish whether a defensive aptation is a true adaptation rather than an exaptation two basic requirements need to be demonstrated. Firstly, that the trait truly is beneficial in the respect postulated, which requires experimental testing; and secondly, that there is a plausible temporal coincidence between the evolution of the trait and that of the supposed selective agent?

Such requirements are not easily fulfilled. Vermeij (1987) outlined five predatory methods, for each of which he listed many different exponents. Different predatory methods may require similar defensive strategies; for example, spines may thwart crushers, borers, prisers and whole animal

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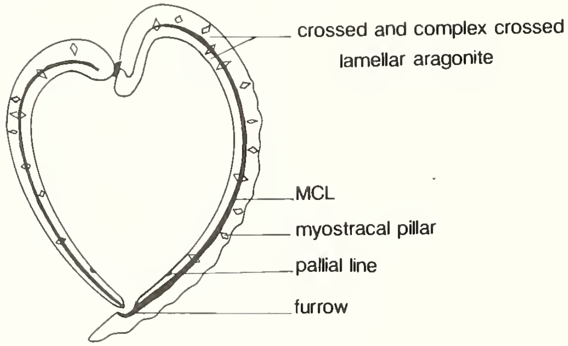
ingesters (Harper and Skelton 1993*a*). The 'sudden' evolution of predators at the beginning of the Mesozoic included large numbers of prising forms (e.g. extra-oral feeding asteroids), and crushing groups (e.g. various crustaceans, nautiloids, fish and reptiles). It may be difficult, therefore, to tie the evolution of a perceived defence to a particular predatory group. There is, however, one type of predation which may be easier to study in this light. The boreholes produced by gastropods (muricids, naticids and marginellids) in their bivalve prey are quite distinct (Carriker and Yochelson 1968; Ponder and Taylor 1992), are easily recognizable in the fossil record, and are distinguishable from other predatory borers (e.g. octopods, see Bromley 1993). This form of predation is quite different from the others enumerated by Vermeij (1987), in that it relies largely upon chemical solution of the shell (see Carriker 1981) rather than physical breaking or forcing apart of the valves. Consequently the defensive requirements against this means of predation are very different (Harper and Skelton 1993*a*). For example, Harper (1991) showed experimentally that the cemented habit provided defence against prising and crushing predators, but in experiments reported by Harper and Skelton (1993*a*) it was found to have no value against boring gastropods. Defences against boring gastropods are also interesting since the evolution of this type of predation occurred late in the MMR. Despite records of gastropod-like boreholes in Triassic bivalves (Fürsich and Jablonski 1984), boring did not become a major cause of death until the Cretaceous, when the first unequivocal naticid and muricid boreholes in bivalves and gastropods are recorded from the Albian Blackdown Greensand of England, where a significant proportion of the fauna is bored (Taylor *et al.* 1983).

This paper concentrates on the evolution of conchiolin sheets within the shells of members of the Corbulidae, a trait which frequently has been referred to as a defensive adaptation against boring gastropods (see below), and seeks to determine whether this is an adaptation or an exaptation.

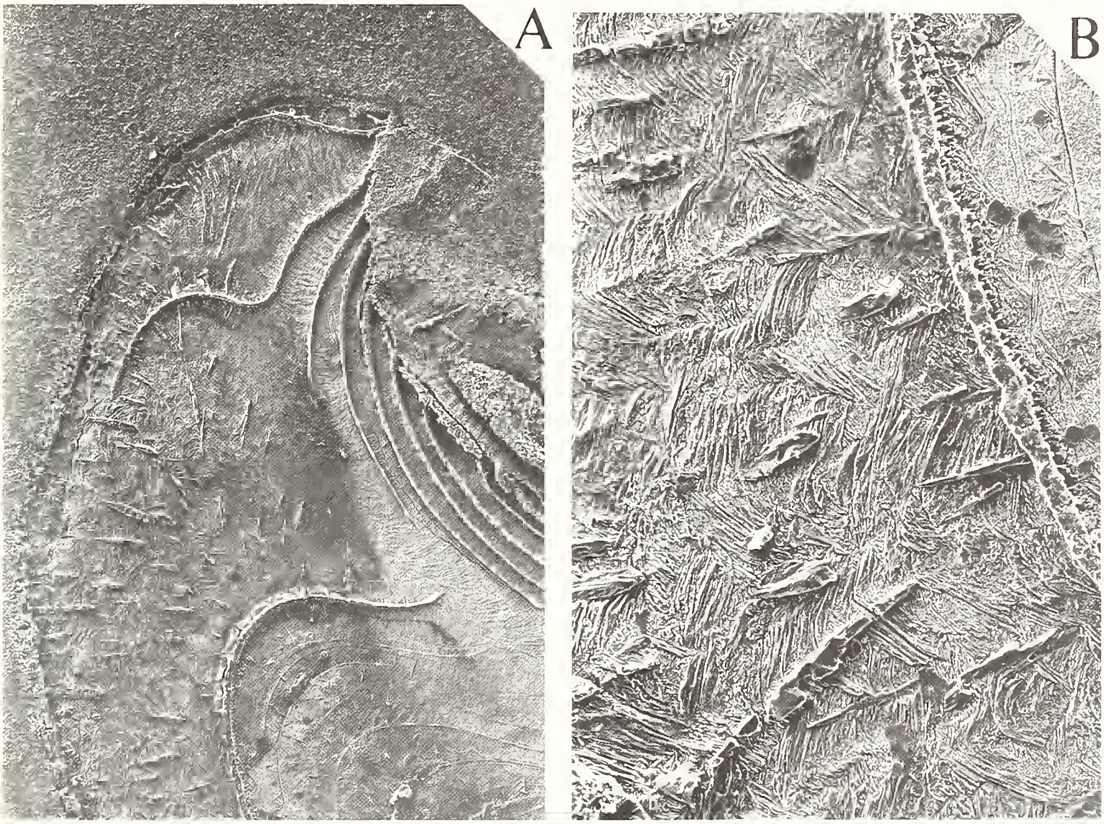


TEXT-FIG. 1. Cross section through a generalized corbulid valve showing microstructure (based on Lewy and Samtleben 1979).

CORBULID BIVALVES

The Corbulidae are small infaunal bivalves with an evolutionary history dating back to the Tithonian (Hallam 1976). The supraspecific taxonomy of the family has been dealt with by Vokes (1945). Traditionally the Corbulidae have been placed within the superfamily Myoidea along with the Myidae and a number of small extinct families (see Newell *in* Moore 1969). However, Morton (1990) pointed out a number of important differences between the corbulids and the Myidae, such as shell structure and anatomical complexity, and suggested that an affinity with the Veneroida is equally likely.

The biology of the corbulids has been described in detail for *Corbula gibba* (Yonge 1946), *C. caribaea* (Stanley 1970) and *C. crassa* (Morton 1990). These living species are sluggish shallow burrowers in a variety of substrates from mud to sandy gravel. They are markedly inequivalve and inequilateral, often with pronounced co-marginal ridges. Morton (1990) regarded them as 'superficially uninspiring' but conceded that one of their redeeming features is their unusual valve microstructure. As described by Taylor *et al.* (1973), both valves are comprised solely of aragonite, with two major units: an outer crossed lamellar layer, and an inner complex-crossed lamellar layer. These layers are separated by the prismatic pallial myostracum and traversed by myostracal pillars. Conchiolin sheets up to 30 μm thick occur within both of these microstructural units and in both valves (Text-figs 1–2). The presence of conchiolin sheets is an unusual arrangement but, contrary to the suggestion of Lewy and Samtleben (1979) and Anderson *et al.* (1991), is not unique to the corbulids; homologous sheets are also found in many oysters (e.g. *Saccostrea cucullata*), corbiculoids, and unioniods (Taylor *et al.* 1969).



TEXT-FIG. 2. Electron micrographs of Recent *Corbula crassa* Reeve, etched to reveal conchiolin sheets; SM X.24528; Hong Kong. A, umbo region; ×44. B, detail of cross lamellar microstructure, MCL and myostracal pillars; ×93.

Conchiolin sheets are of two types: the main conchiolin layer(s) (MCL) which cover(s) the entire surface of the valve, and more numerous lesser sheets which are less continuous with a more patchy distribution. In *Corbula crassa* Morton (1990) recognized around twenty of the secondary sheets, particularly in the postero-ventral region. Rather than being formed by entrapment of the periostracum within the shell, as suggested by Yonge (1946) and Taylor *et al.* (1973), Morton found conchiolin to be secreted periodically by the outer surface of the mantle lobe, alternately with aragonite. The presence of the MCL within the shell represents a line of weakness. Decay of this organic layer frequently leads to splitting of the valves (Lewy and Samtleben 1979; de Cauwer 1985). Lewy and Samtleben noted that such taphonomic splitting has caused considerable taxonomic problems where the separated portions of the valves have been described as different species or even different genera.

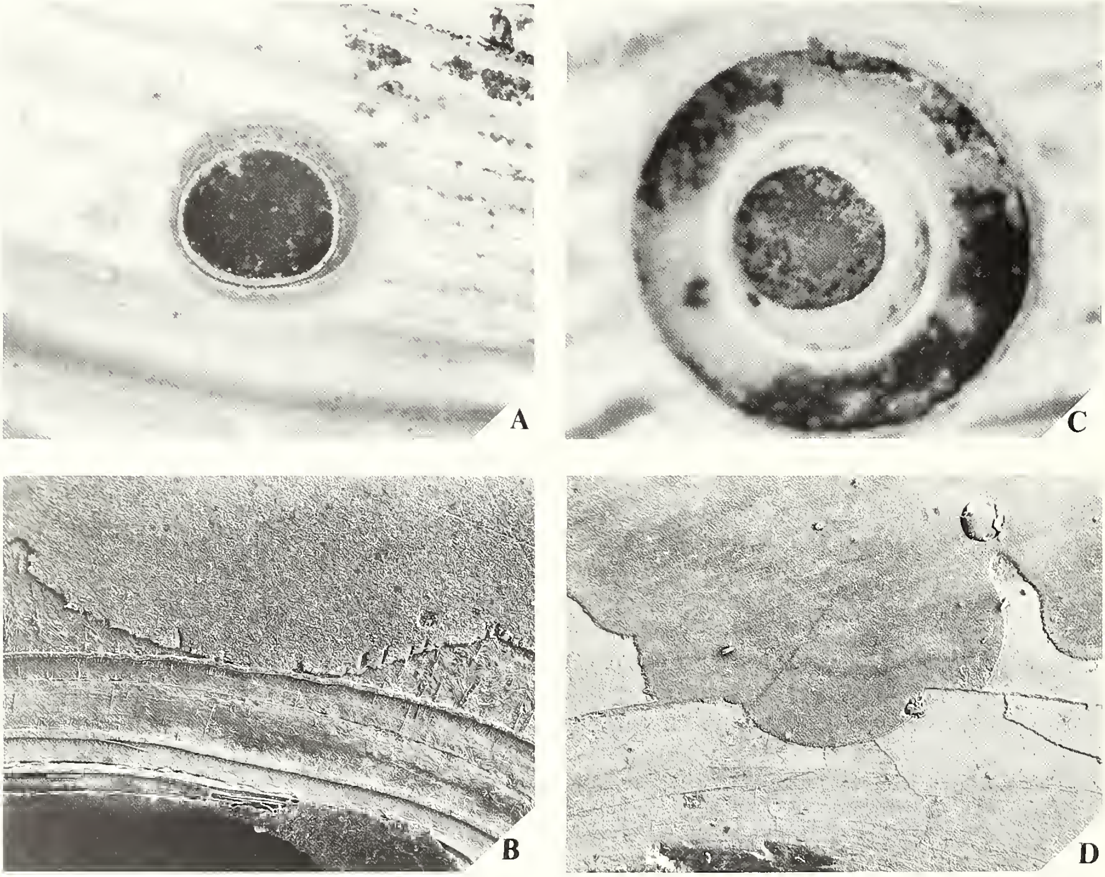
WHAT IS THE PRIMARY FUNCTION OF THE SHEETS?

Defensive value

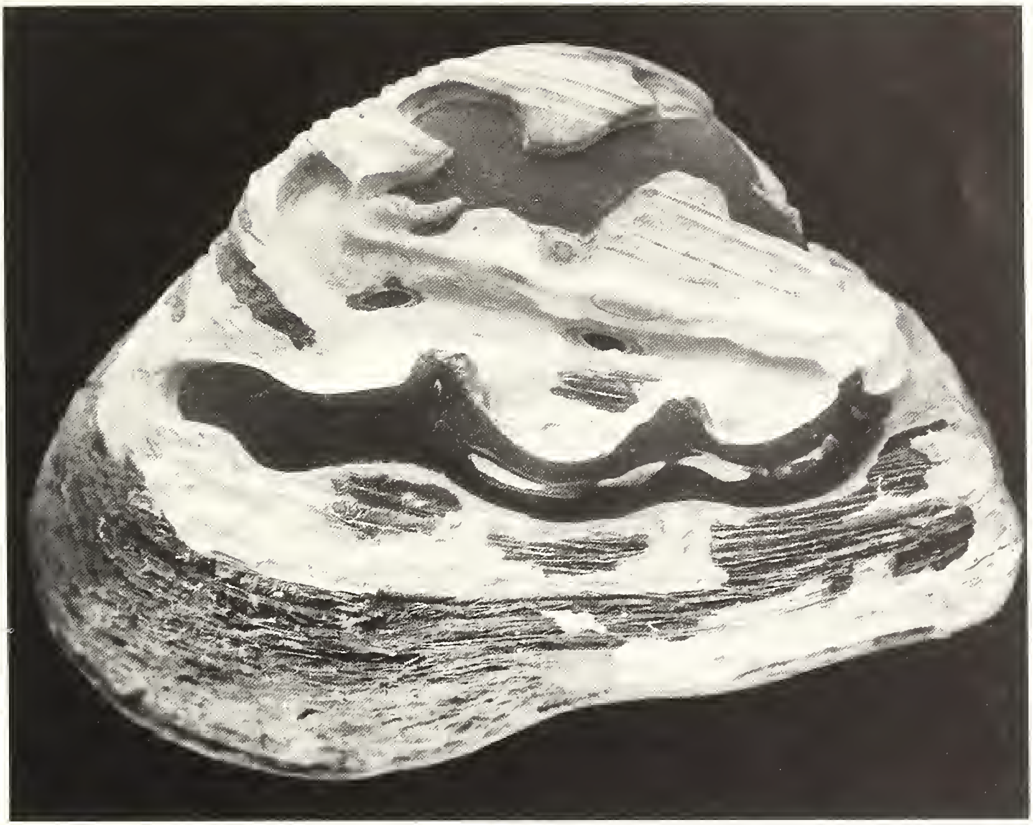
It has long been suggested that conchiolin sheets have a defensive value against boring predators. Jeffreys (1865, p. 65) noted that in *C. gibba*, 'the shell is subject to the attacks of predatory molluscs, which do not always succeed in perforating it; in such cases the white outside layer only is removed, exposing the succeeding layers, which are of a firmer texture and coffee coloured ...'. Since then, this possibility has been explored by many authors (e.g. Ziegelmeier 1954; Fischer 1963; Lewy and Samtleben 1979; Morton 1990).

Evidence for the defensive value of the conchiolin sheets

There seems to be little doubt that the conchiolin sheets of corbulids act as a defence against boring predators. The above authors illustrated numerous examples of corbulid shells scarred by incomplete boreholes which terminate at such sheets (see also Text-fig. 3). Carriker (1981) recounted that both naticids and muricids bore largely by using a chemical secretion of acids, enzymes and



TEXT-FIG 3. Failed predatory boreholes in Recent *Corbula crassa* Reeve; Hong Kong. A–B, termination of a borehole at MCL. A, plan view; SM X.24545; × 14. B, cross section; SM X.24528; × 22. C–D, boreholes which pass through the MCL (with a restricted diameter) but terminate at a subsequent conchiolin sheet. C, plan view; SM X.24546; × 14. D, cross section; SM X.24528; × 32.



TEXT-FIG. 4. Non-predatory borings in a Recent *Corbula crassa* Reeve in which the damage is restricted to the outer shell layers by the MCL; SM X.24554; Hong Kong; ×5.

chelators delivered by the accessory boring organ (ABO). Gabriel (1981) experimented on the effectiveness of ABO secretion on various bivalve shell microstructures, and found that those with a high organic content are least susceptible, whilst Harper and Skelton (1993*b*) showed experimentally that mytilids deprived of their thick periostraca (of similar composition to the conchiolin sheets) are much more vulnerable to muricid boring; they speculated that infaunal bivalves with thick periostraca might gain a similar protection from naticid gastropods. It is thus evident that the conchiolin sheets are more resistant to the action of ABO secretion than the calcareous parts of the shell, and hence act as a barrier. This is further evidenced by the observation that where the borer successfully breaches a conchiolin sheet the borehole produced is frequently of reduced diameter (see Text-fig. 2C–D).

Taylor (1990) examined the effect of similar sheets in the oyster *Saccostrea cucullata* on their muricid predators in Hong Kong. Taylor demonstrated that ninety five per cent of failed boreholes terminate at the sheets, and that even those which are successful in penetrating are of notably reduced diameter; he also discovered that muricids studied in the act of boring were most frequently in the process of boring through the sheet, implying that boring the conchiolin sheet is a more time consuming process than boring the calcareous parts of the shell.

Analysis by Kelley (1988) showed that patterns of naticid predation of Miocene corbulids do not fit the elaborate models of predicted foraging proposed by Kitchell *et al.* (1981). Kelley explained this by the presence of the conchiolin sheets. However, Anderson *et al.* (1991) and Anderson (1992) suggested that other factors (e.g. small prey size, small sample sizes and environmental factors) have led to these unpredictable patterns and indeed claimed that the conchiolin sheets do not retard boring. Evidently Anderson and co-workers were unaware of the work of Gabriel (1981), Taylor (1990) and Morton (1990). Arguments over whether predation of corbulids is stereotypic or non-stereotypic are not the primary concern of this paper, although its conclusions may have some bearing on that debate.

Alternative hypotheses

Several alternative hypotheses may be advanced for the primary function of the conchiolin sheets.

1. Retarding shell solution. Corbulids are frequently associated with low salinity and cold bottom water conditions, both of which may be undersaturated with respect to calcium carbonate and likely to cause shell dissolution (Lewy and Samtleben 1979; Maslin 1989). The presence of thick organic sheets within the calcareous valve may retard acidic attack and loss of shell material. Previous studies have invoked this selective advantage for the thick periostracum and homologous conchiolin sheets in the freshwater unionids, margaritiferids and corbiculids (Tevesz and Carter 1980; Kat 1983; Isaji 1993).

2. Assistance with hermetic sealing. Members of the Corbulidae are renowned for their physiological tolerance; for example they may survive short periods of low oxygen levels (Lewy and Samtleben 1979). Morton (1990) noted that *Corbula crassa* survives in the highly polluted waters of Tolo Channel in Hong Kong, whilst other bivalves have disappeared. Tolerance of physiologically 'difficult' conditions appears to have persisted throughout the evolutionary history of the group; Hallam (1976) uses the Jurassic *Corbulolimima* as an indicator of low brachyhaline conditions and they are often found in monotypic assemblages (e.g. *Corbula* bed in the Thanet Sands). Apart from the low metabolic requirements of these sluggish animals, part of their success must be ascribed to the ability to produce a tight hermetic seal when the valves are closed. Lewy and Samtleben (1979) noted that, when closed, the ventral edge of the smaller left valve is placed within the groove in the right valve in which the MCL crops out (Text-fig. 1), thus forming an 'elastic gasket, permitting hermetic closure of the valves'. It seems likely that the elastic nature of the conchiolin sheet would enhance a tight seal.

3. Protection against non-predatory borers. The activities of non-predatory boring organisms (e.g. worms, sponges, forams, algae and fungi) may severely weaken calcareous shells (Kent 1981). As with predatory boring, the conchiolin sheets appear to retard the boring activity and confine damage to the outer shell layer (Text-fig. 4). Korringa (1951) regarded the analogous conchiolin sheets in *Ostrea edulis* as affording protection from damage by polydorid worms.

4. Prevention of crack propagation. Anderson (1992) suggested that the conchiolin sheets prevent the propagation of cracks within the shell and may, therefore, be defensive against crushing predation. However, it has not been demonstrated that the sheets do function in this way and there is little evidence of shell repair in Recent or fossil corbulids (but see Robba and Ostinelli 1975) nor are there any published accounts of corbulids being important in the diets of crustaceans. Study of Recent corbulids did not reveal examples in which cracks had been deflected along the conchiolin sheets.

Discriminating between competing hypotheses

With the exception of the last, evidence can be cited in support of each of the above putative functions for the conchiolin sheets, but are these more important than their defensive value? The hypothesis tested here is that conchiolin sheets in corbulids evolved as a direct response to boring predation and that other benefits derived from these sheets are secondary. Three different approaches have been used: (i) charting the success rate of gastropod borehole attack on corbulids over geological time; (ii) using various microstructural, morphological and taphonomic features to trace the evolutionary history of conchiolin sheets; and (iii) examining the geographical distribution of conchiolin sheets in Recent corbulids. The first and second methods hinge upon determining if pre-Albian corbulids possessed conchiolin sheets or whether their appearance post-dates the evolution of boring in the gastropods. If it can be demonstrated that conchiolin sheets are found in corbulids before the onslaught from boring gastropods, it implies that any defensive value against these predators is secondary. The third method assumes that the selection pressure for the various functions will vary latitudinally. Dudley and Vermeij (1978) found that the boring frequency in low latitude turritellids is approximately three times that in higher latitudes, a general trend which was confirmed by Allmon *et al.* (1990). Although Vermeij *et al.* (1989) observed an equatorward decrease in boring predation of bivalves, their data were limited to small sample sizes with few temperate taxa and tropical taxa, largely from Panama. Taylor and Taylor (1977) found that the diversity of predatory gastropods in the eastern Atlantic increased equatorwards. Both these observations suggest that selection pressure favouring defensive adaptations against boring predators increases towards the tropics. Conversely, selection pressure favouring anti-shell dissolution is strongest poleward, as calcium carbonate is most soluble in cold water.

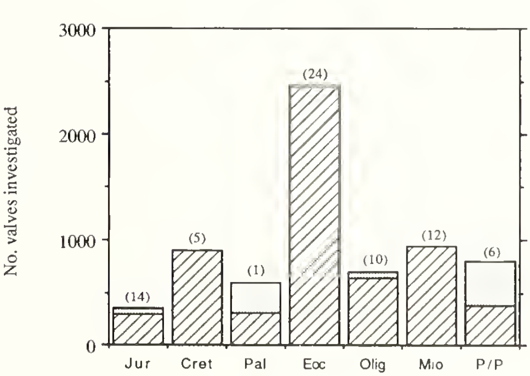
MATERIALS AND METHODS

Borehole survey

This survey was run similarly to that conducted by Allmon *et al.* (1990) in their investigation of the evolutionary history of drilling and peeling of turritellids.

The collections of the Sedgwick Museum, University of Cambridge (SM) were scoured for specimens belonging to the family Corbulidae. The computer listings (Price 1984) were searched for the generic and subgeneric names *Aloidis*, *Anisocorbula*, *Bicorbula*, *Carycorbula*, *Corbula*, *Corbulomima*, *Eocallista*, *Jurassicorbula*, *Lentidium* and *Varicorbula*. Despite large holdings of corbulids, the sample sizes for the Paleocene, Oligocene, Pliocene and Pleistocene were comparatively small and thus were supplemented by examining the collections of The Natural History Museum (London) (Text-fig. 5). Internal and external moulds were rejected, as were individuals which had split along the conchiolin sheet in the manner described by Lewy and Samtleben (1979). The latter were discarded because de Cauwer (1985) has observed that taphonomic splitting along the MCL of valves bearing failed boreholes results in the production of

TEXT-FIG. 5. The number of corbulid specimens from each geological time interval examined for this study. Specimens from the Sedgwick Museum (Cambridge) are depicted by striped shading and those from The Natural History Museum (London) by dotted shading. The numbers in brackets refers to the number of species represented in each time interval.



two 'valves': one bearing a complete borehole, the other apparently unscarred, leading to serious distortion of palaeoecological interpretations. Split valves were identified by their smooth reflective external surfaces which lack appreciable ornament or, on internal surfaces, by the absence of the adductor musculature. Specimens in blocks were used only as qualitative evidence, as it is not possible to determine whether these boreholes perforate the valve or not.

After this winnowing procedure, the remaining valves were retained for closer inspection. Each valve was examined for signs of boreholes, both complete and incomplete. Doubtful holes were rejected. For each scarred valve, the following were recorded: valve height, whether the valves were articulated or single, number of boreholes present, whether each of these was complete or incomplete, and whether it occurred on the right or left valve. The diameter of the boreholes was measured using vernier calipers, their position was marked on a species outline, and borehole morphology noted.

For each species, it was then possible to note the number of bored and unbored valves. Inevitably, any study which is heavily dependent on museum collections will be charged with biases. Collector bias may alter severely the frequency of bored and unbored specimens represented in a collection; relative abundances may be skewed by the number of boreholes being enhanced or reduced by collectors who regard their presence as novelty or blemish. However, these problems are minimized by the large number of individuals examined, the large number of different contributors and the small size of bivalves, many of which were collected in large lots.

Other authors have published information on boreholes in corbulids. These data were also considered, but there are considerable problems with utilizing this information when it is unclear exactly how the data were acquired or how derived information was calculated (de Cauwer 1985). Only data which had been collected in a manner similar to the above were used.

Geographical distribution of conchiolin sheets

Specimens of sixteen species of Recent corbulids, selected from as wide a geographical range as possible, were extracted from the collections of The Natural History Museum (London). These were blocked in epoxy resin, cut along the maximum growth axis, polished and then etched slightly in dilute hydrochloric acid. They were then gold-sputtered for routine scanning electron microscopy (SEM), using a JEOL JSM-820. Blocks were then examined for the presence or absence of conchiolin sheets, and where present their distribution, appearance, number and thickness were recorded.

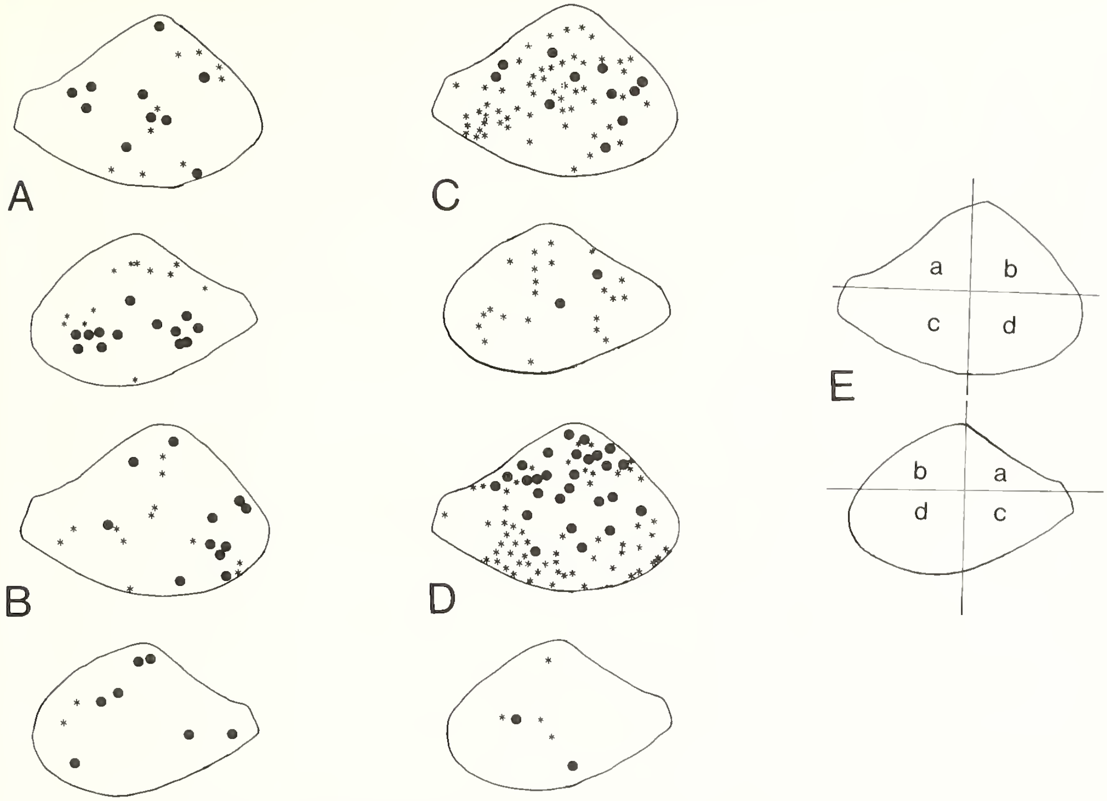
Temporal appearance of the conchiolin sheets

Three different methods have been used to determine whether fossil specimens possessed conchiolin sheets.

Direct microstructural evidence. Selected specimens from a range of geological ages were prepared for SEM in the manner described above and the same observations recorded. Additionally, some of the blocks were cut into thin slices, polished and carbon coated for X-ray micro-analysis (LINK 10000).

Taphonomic evidence. The presence of taphonomic splitting provides a good indication of the presence of the MCL. For each species examined, the occurrence of individuals in which splitting had occurred was noted. De Cauwer (1985) took the rather gloomy view that taphonomic splitting seriously limited the potential of palaeoecological studies of corbulids, but in this case it can be utilized in a positive way.

Morphological evidence. The occurrence of the MCL may be inferred by the presence of a co-marginal furrow in the right valve which runs ventrally to the pallial line (Text-fig. 1). This furrow marks the point on the internal surface where the MCL crops out, and also where the ventral margin



TEXT-FIG. 6. The positions of successful (*) and failed (●) boreholes in the four most preyed upon taxa. A, *Corbula regulbiensis* Morris; Paleocene; data from the Sedgwick Museum only. B, *C. alabamiensis* Lea; Eocene. C, *C. pisum* Sowerby; Eocene. D, *C. gibba* (Olivi); Miocene. E, the division of the corbulid valves into four sectors; the areas covered by each sector are a = 21 per cent, b = 22 per cent, c = 26 per cent and d = 31 per cent.

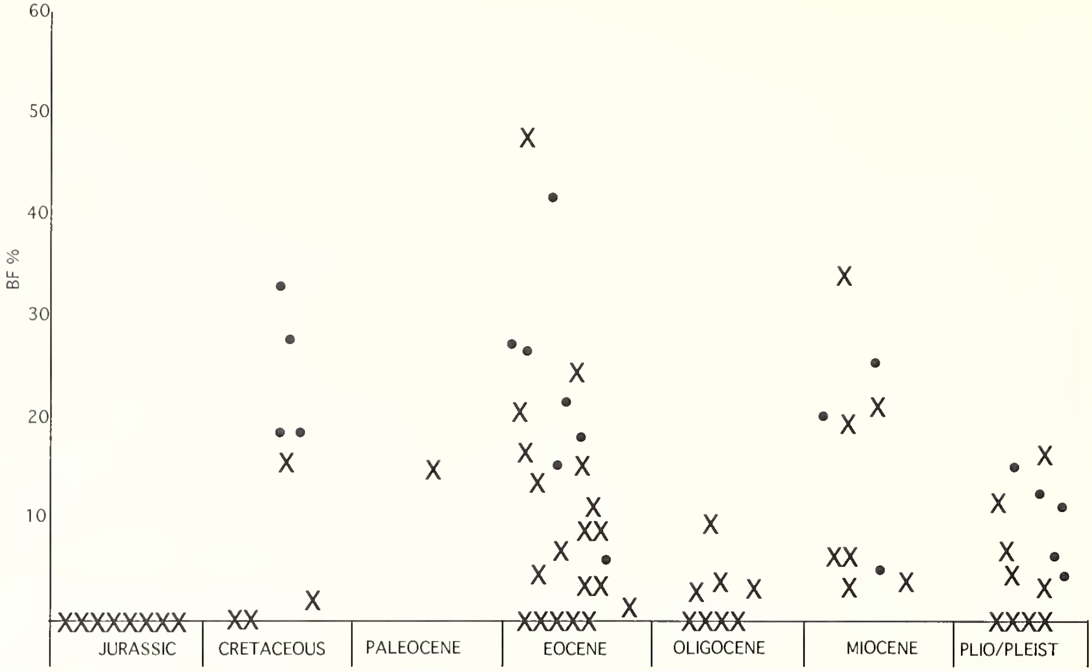
of the left valve resides during adduction (Lewy and Samtleben 1979). Each of the species examined during the borehole survey were inspected and the presence or absence of the furrow noted. Although Lewy and Samtleben used the furrow to indicate the presence of the MCL in Cretaceous corbulids, to do so on the basis of their Recent spatial coincidence may not be sound.

All mounted specimens used for SEM are now held in the Sedgwick Museum Cambridge (SM X.24504–SM X.24544, SM X.24554.

RESULTS AND ANALYSES

Borehole survey

After rejection of unsuitable material, a total of 6834 valves belonging to 72 species were examined. The raw data derived from this survey are presented in Appendix 1. Additional data culled from previous work are shown in Appendix 2. Except for the work of Taylor *et al.* (1983) on the Albian Blackdown Greensand, there is no overlap between the species and localities explored in the present study and those of previous studies. Since Taylor *et al.* made some of their observations on Sedgwick Museum material, my data set is a sub-set of theirs and thus, in the ensuing analysis, their data for this time have been used instead.



TEXT-FIG. 7. Boring frequency recorded from corbulid prey over geological time. Each corbulid species from each horizon is plotted as a single point; X = data from this survey and ● = data from previously published surveys.

Following Vermeij *et al.* (1989) for the statistical analyses, only samples comprising of ten or more valves were used to determine boring rates, and only species in which there were at least ten boring attempts were used to calculate failure rate.

General observations on gastropod predation of corbulids. As reported in most previous studies on corbulids, right valves were more often bored than the left (although Morton (1990) discovered a preference for the left valve of *Corbula crassa*) and in many cases this preference was statistically significant by the χ^2-test (see Appendix 1). This observation may be partly explained by the fact that the right valve has a larger surface area than the left, but most of this increased area is 'unavailable' to the borer as it corresponds to the broad ventral flange where there is no overlap with the left valve. There were no significant instances of the left valve being bored more often than the right. The preference for right valve boring was present in *Corbula elegans* and thus was established early in the history of boring predation. Apart from this valve preferences, boreholes appeared to be randomly scattered except for a general aversion to the extreme ventral margins of the discordant right valve. Text-figure 6 illustrates the borehole positions found on the four most attacked species: *Corbula regulbiensis* (Palaeocene), *C. alabamiensis* (Eocene), *C. pisum* (Eocene) and *C. gibba* (Miocene). The surface of the valves was divided into four unequal sectors and the number of all boreholes occurring in each was counted. Division into a greater number of sectors, as used by Kelley (1988) and Anderson *et al.* (1991), was considered unwise for this taxon as most of the species here considered are small (valve height < 10 mm); with a higher number of sectors it is difficult accurately to locate boreholes, particularly in cases where the hole is relatively large. A χ^2-test tested the null hypothesis that borehole siting was random with the expectation that the number of holes in each sector would be proportional to its area. For none of these taxa was it possible to reject the null hypothesis, thus agreeing with previous assertions that naticid predation of corbulids is non-stereotyped (Kelley 1988).

Most of the boreholes examined had the paraboloid shape of the type created either by naticids (Carriker and Yochelson 1968) or marginellids (Ponder and Taylor 1992). Relatively few were more straight sided of the type generally attributed to muricids (Carriker and Yochelson 1969), although as pointed out by de Cauwer (1985), muricid holes passing through a conchiolin sheet have a restricted diameter giving the borehole a stepped appearance which may be mistaken for naticid (or marginellid) predation. As corbulids are infaunal burrowers their principal gastropod predators are liable to be naticids or marginellids, although, since they only reach shallow depths it is not unlikely that if wholly or partially exhumed they may fall prey to epifaunal muricids. Morgan (1972) showed that dogwhelks deprived of their normal epifaunal prey (mussels and barnacles) attack infaunal cockles. It is interesting to note that Taylor (1970) identified muricid holes in Eocene *Bicorbula gallica* and that these were concentrated towards the posterior (i.e. closest to the sediment/water interface), although Morton (1990) recorded that Taylor by then believed these to be naticid borings.

Temporal changes in boring. Although it would be optimal to gauge changing boring rate by calculating the predation rate (PR), a measure of the number of boreholes per bivalved individual, as used by some other authors (e.g. Taylor *et al.* 1983), it is impractical here as most of the specimens in this study were disarticulated. A more practical approach has been to use boring frequency (BF), the percentage of valves examined bearing either complete or incomplete boreholes (some authors, e.g. de Cauwer (1985), use a different definition of this parameter, using only the percentage of valves displaying complete boreholes). Text-figure 7 plots the BF over geological time. Each species from each locality is plotted as a single point. I chose not to plot a singe mean BF for each period, as used by Allmon *et al.* (1990), as the value obtained at each locality is liable to depend on a number of factors: predator presence, presence of other more preferable prey, as well as the susceptibility of the corbulids themselves. Vermeij (1982) pointed out that different localities and environments will produce different BF values for the same taxa.

No boreholes were found in pre-Albian corbulids. Albian boreholes were noted from the Blackdown Greensand as well as in blocked samples of the Gault containing *Corbula gaultina* (e.g. SM B.13693–13699). There is a significant difference (two tailed *t*-tests, $P < 0{\cdot}01$) between the boring frequencies noted for Early and Late Cretaceous corbulids. Although the Early Cretaceous values come solely from the Blackdown Greensand (other Early Cretaceous samples pre-date the Albian) it should be noted that according to Taylor *et al.* (1983) corbulids are both the most abundant bivalve family and the most frequently attacked prey in that fauna.

In the Tertiary, BF shows wide variation with many species apparently suffering little predation and others where the pressure was more extreme. The highest BF was recorded in the Eocene *Corbula costata* from the Barton Clay at forty eight per cent.

The Permutation Test (Siegel and Castellan 1988) was used to test for significant differences between recorded BF for each geological time-interval. There was no significant difference (at the five per cent level) between the BF of any consecutive interval, except for between the Eocene and Oligocene. This significant difference is probably due to the small Oligocene data set, although it is of note that Allmon *et al.* (1990) also found an Oligocene drop in BF although again the sample size is low.

Failed boreholes and multiply bored valves. All boreholes which terminated before reaching the internal surface of the valve were classified as failed. This study does not follow Kitchell *et al.* (1986) and Kelley (1988), in designating some complete boreholes as non-functional and thus also as failures. These authors designated complete boreholes in which the ratio of inner and outer borehole diameter is less than 0·5 as non functional on the basis of experimental work by Kitchell *et al.* (1986), which showed that *Terebra dislocata* could not feed through such a restricted opening. It is not yet known, however, how general this value is nor whether it is applicable here. In any case, in natural

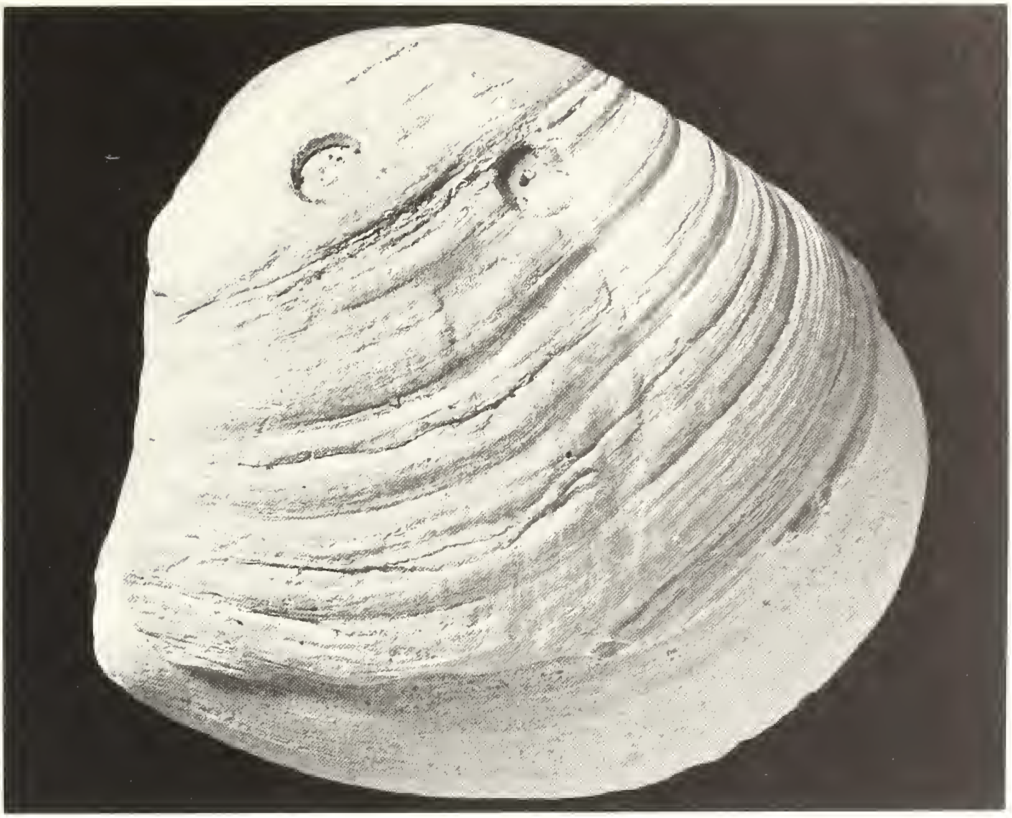
TABLE 1. Failure rate of boreholes calculated as by Vermeij (1987) and Vermeij *et al.* (1989). Those marked by symbols have been calculated from previously published data: ‡ = Anderson *et al.* (1991), * = Vermeij 1987), † = Cauwer (1985) and § = Adegoke and Tevesz (1974).

	Species	Locality	Failure rate
Plio/Pleistocene	*Varicorbula caloosae* (Dall)	Sarasoto	0·12‡
	V. caloosae	Davis	0·07‡
	V. caloosae	Forsberg	0·03‡
	V. caloosae	Punta Gorda	0·13‡
	Corbula gibba (Olivi)	Nicosia	0·40
	C. inaequalis Say	South Carolina	0·23
	Carycorbula spp.	Virginia	0·53*
Miocene	*C. carinata* Dujardin	Bordeaux	0·34
	C. gibba	Gironde	0·54
	C. gibba	Mellesdorf	0·86†
	C. sericea (Dall)	Bowden	0·33
Oligocene	*C. vectensis* Forbes	Isle of Wight	0·00
Eocene	*C. alabamiensis* Lea	Alabama	0·58
	C. costata (Sowerby)	Barton Beds	0·85
	C. cuspidata Sowerby	Barton Beds	0·20
	C. cuspidata	Headon Beds	0·19
	C. murchisoniana Lea	Alabama	0·53
	C. pisum Sowerby	Barton Beds	0·14
	C. pisum	Headon Beds	0·41
	C. brabantina Vincent	Oedelem	0·10†
	C. rugosa Lamarck	Parnes	0·33†
	C. rugosa	Grignon	0·41
	V. amekiensis (Eames)	Nigeria	0·11§
Paleocene	*C. regulbiensis* Morris	Thanet Sands	0·52
Cretaceous	*C. crassiplica* (Gabb)	Coon Creek (Camp.)	0·22†
	C. crassiplica	Mercers Hill (Camp.)	0·34†
	C. substriatula d'Orbigny	Vaals (Camp.)	0·23†
	Corbula elegans Sowerby	Blackdown (Albian)	0·00

conditions, even such a small complete perforation may be fatal even if it is abandoned, such as by metabolite leakage either attracting other predators or weakening the bivalve.

A total of 190 failed boreholes was observed. It is probable that some of the complete boreholes which occur close to the ventral edge of the right valve could have passed harmlessly through without penetrating flesh, and thus were also failures. However, it is not possible to be certain of these and, in any case, these failures cannot be attributed to the presence of conchiolin sheets. Table 1 lists failure rate for each of the major prey species studied. Following Vermeij (1987) and Vermeij *et al.* (1989) failure rate is expressed as a proportion (number of incomplete boreholes to total number of boreholes). In only *Corbula elegans* and *C. vectensis* were no failed boreholes observed; although failures were observed in the former by Taylor *et al.* (1983), they do not give sufficient data to calculate a proportion.

Most failed boreholes were shallow, penetrating less than half of the valve thickness. Most were flat bottomed lacking the characteristic central boss of incomplete naticid holes noted by Carriker and Yochelson (1968) and in many of these, termination of the hole coincides with intersection with

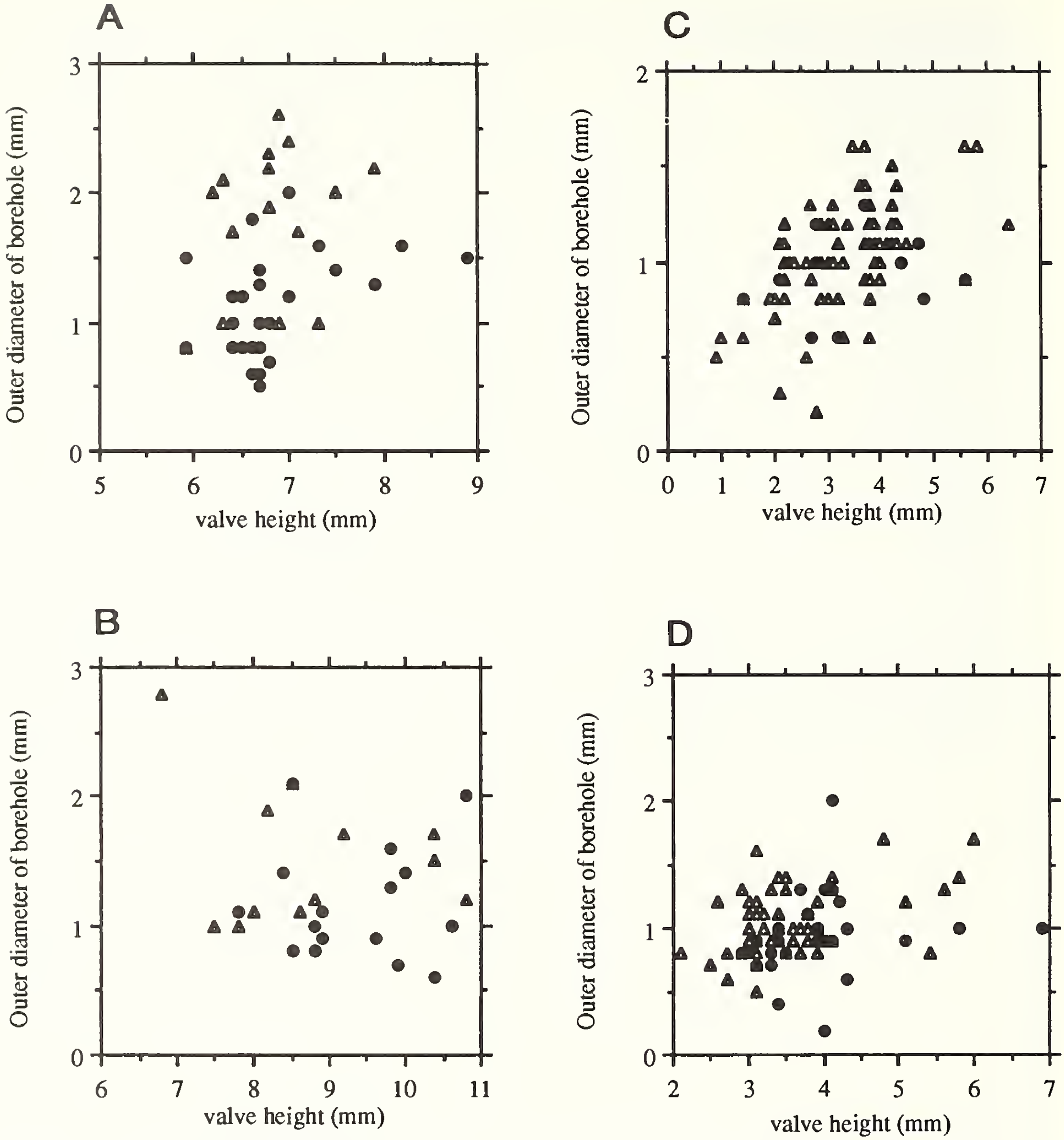


TEXT-FIG. 8. *Corbula idonea* bearing two failed boreholes; SM C.34210; Maryland; Miocene; the floor of the holes are flat bottomed rather than bossed, and are terminated at the level of the MCL, indicated by taphonomic splitting; × 3.

a conchiolin sheet (Text-fig. 8). In other cases, boreholes terminated in the calcareous part of the shell having passed through, and been much restricted, by the conchiolin sheets.

Taking into account the preference for boring the right valve, the data from the seven species with more than ten failed boreholes were analysed by χ^2-test taking the null hypothesis that failure occurs equally on right and left valves. Contrary to de Cauwer's (1985) assertion that failures occur more frequently on the left valve, no significant difference was found at the five per cent level. In order to determine whether failed boreholes occur randomly or are concentrated over specific parts of the valves, the tests for stereotyped borehole positioning used earlier were repeated this time using only the data for failed boreholes. No significant departures from the null hypothesis were found for three of the species but for Miocene *Corbula gibba* there were significantly higher numbers of failed boreholes in the more dorsal sectors ($P < 0{\cdot}01$).

Kelley (1988) suggested that most failed boreholes resulted from small predators attempting prey items which were too large. There is no evidence for such over-ambition here. Using Wiltse's (1980) idea that predator size may be gauged from borehole size, the outer diameter of successful boreholes was plotted against valve height for the four most preyed upon species (Text-fig. 9). Although the correlation coefficients are not high, it does seem generally that larger prey was taken by the larger gastropods (although these larger predators will also take smaller items). Plotting the same information for failed boreholes reveals no notable differences and no evidence that they occur as smaller boreholes in larger prey. Failure was clearly due to another factor.



TEXT-FIG. 9. Valve height of victim plotted against the outer borehole diameter of successful (triangles) and failed (circles) boreholes. A, *Corbula regulbiensis* Morris; Paleocene; data from the Sedgwick Museum only; $\log y = 1{\cdot}4 \log x - 0{\cdot}9$, $r = 0{\cdot}3$. B, *C. alabamiensis* Lea; Eocene; $\log y = -0{\cdot}29 \log x + 0{\cdot}43$, $r = 0{\cdot}13$. C, *C. pisum* Sowerby; Eocene; $\log y = 0{\cdot}49 \log x - 0{\cdot}25$, $r = 0{\cdot}5$. D, *C. gibba* (Olivi); Miocene; $\log y = 0{\cdot}5 \log x - 0{\cdot}26$, $r = 0{\cdot}3$.

Has the proportion of failed attacks changed over geological time? Statistical analysis by the Permutation Test reveals no significant difference (at the five per cent level). The probability of failure was as high in the Cretaceous as in the subsequent periods. Indeed, from the Albian Blackdown Greensand, sixty six per cent of boreholes observed in *Corbula truncata* were failed, and

TABLE 2. The distribution of conchiolin sheets in Recent corbulids taken from a wide geographical range.

Species	Locality	Valve height (mm)	No. of major sheets	Maximum sheet thickness (μm)
60°–40°				
Corbula gibba (Olivi) SM X.24530	Millport, Scotland	8·5	1	< 10
C. nucleus Lamarck SM X.24540	Naples, Italy	7·5	1	30
A. mediterranea da Costa SM X.24531	S. of Rome, Italy	7·0	1	5
40°–20°				
C. sp. SM X.24537	Victoria, Australia	12·8	1	$\leqslant 10$
C. sp. SM X.24543	Suez	16·0	0	—
C. crassa Reeve SM X.24528	Hong Kong	—	2	18
C. porcina Lamarck SM X.24535	Montevideo, Uruguay	14·3	0	—
Notocorbula zealandica Quoy and Gaimard SM X.24532	Doubtless Bay, New Zealand	8·1	3	10
Anisocorbula venusta (Gould) SM X.24539	Honshu, Japan	6·0	4	10
Varicorbula notalis (Hinds) SM X.24545	Kyushu, Japan	4·8	1	8
C. truncata (Hinds) SM X.24531	Port Jackson, Australia	18·9	3	10
20°–0°				
C. acutangular Gray SM X.24533	Aden	7·1	3^+	< 10
C. sp. SM X.24536	Queensland, Australia	10·7	1	12·5
Aloidis dautzenbergi (Lamarck) SM X.24538	Sierra Leone	11·0	2	10
A. sulcata (Lamarck) SM X.24541	Sierra Leone	15·1	1	30
A. trigona Hinds SM X.24542	Sierra Leone	9·5	1	10

from the same lithology Taylor *et al.* (1983) reported a single specimen of *C. elegans* bearing six incomplete boreholes.

Relatively few of the holed valves (seven per cent) had more than one borehole per valve. The vast majority of these multiply bored valves had only two boreholes with a maximum of three in two specimens. Kitchell *et al.* (1986) reserve the term 'multiple boreholes' for valves punctured by more than one complete perforation. Only two examples of this phenomenon were found, both in individuals of Miocene *Corbula gibba* bearing two complete holes each (both of which would have been deemed functional by Kitchell *et al.* 1986). A broader definition of 'multiple boreholes' is more useful when applied to an articulated specimen bearing more than one borehole (successful or failed) because these give an indication of the number of predation attempts per individual. Unfortunately, taphonomic and preparation processes limit this information; most holed specimens were disarticulated. However, of the eighty articulate bivalved specimens which did bear holes only seven were bored more than once, implying that few corbulids experienced more than one attack.

Geographical patterns in conchiolin sheets

The results of the survey of conchiolin sheets in Recent corbulids are shown in Table 2. In only two of the species did the specimens examined apparently lack conchiolin sheets (*Corbula* sp. from Suez, and *C. porcina* from Uruguay). In all others the basic distribution of major and subsidiary sheets was as described by Morton (1990) for *C. crassa*. It might be anticipated that major sheets would be more numerous in larger (and hence thicker) individuals, but this is not supported here. There is no clear latitudinal trend in the numbers of sheets observed, and no evidence that higher latitude taxa are better endowed. Although several of the low latitude specimens do show more conchiolin layers than those from higher latitudes, this is not statistically significant.

TABLE 3. Results of the direct microstructural survey of the preservation of conchiolin sheets in fossil corbulids. See also Plate 1.

Species	Age	Specimen details	Description of sheets
Corbula gibba (Olivi)	Holocene	Holland, SM X.24529	MCL very thin, < 10 mm (Pl. 1, fig. 1)
C. striata Walker and Boys	Pliocene	Suffolk, UK, SM X.24526	MCL present, *c.* 10 µm
C. inaequalis Say	Pliocene	S. Carolina, USA, SM X.24525	MCL present, < 10 µm
C. carinata Dujardin	Miocene	Bordeaux, France, SM X.24524	At least three major sheets, > 10 µm (Pl. 1, fig. 2)
C. gibba	Miocene	Bordeaux, France, SM X.24523	MCL very thin, < 10 µm
C. sericea (Dall)	Miocene	Jamaica, SM X.24522	None observed
C. vectensis Forbes	Oligocene	Isle of Wight, UK, SM X.24521	None observed
C. alabamiensis Lea	Eocene	Alabama, USA, SM X.24520	At least three major sheets, up to 20 µm (Pl. 1, fig. 5)
C. costata (Sowerby)	Eocene	Barton, UK, SM X.24519	At least four major sheets, > 10 µm
C. cuspidata Sowerby	Eocene	Barton, UK, SM X.24518	MCL visible to naked eye, > 10 µm
C. ficus (Solander)	Eocene	Barton, UK, SM X.24517	At least three major sheets, MCL visible to the naked eye, > 10 µm (Pl. 1, fig. 3)
C. murchisoniana Lea	Eocene	Alabama, USA, SM X.24516	MCL visible to the naked eye, > 20 µm (Pl. 1, fig. 4)
C. pisum Sowerby	Eocene	Barton, UK, SM X.24515	Vestiges of thin MCL < 5 µm
C. regulbiensis Morris	Paleocene	Thanet, UK, SM X.24514	MCL present, *c.* 10 µm
C. crassiplica (Gabb)	Cretaceous (Maastrichtian)	Georgia, USA, SM X.24527	MCL present, *c.* 10 µm
C. angulata (Phillips)	Cretaceous (Neocomian)	Specton, UK, SM X.24513	None observed
C. elegans Sowerby	Cretaceous (Albian)	Blackdown, UK, SM X.24512	Silicified material, no sheet preservation
C. gaultina Pictet and Campiche	Cretaceous (Albian)	Folkestone, UK, SM X.24511	None observed
C. striatula Sowerby	Cretaceous (Albian)	Atherfield, UK, SM X.24510	None observed
C. truncata Sowerby	Cretaceous (Albian)	Blackdown, UK, SM X.24509	Silicified material, no sheet preservation
C. chilmarkensis Cox	Jurassic (Portlandian)	Tisbury, UK, SM X.24508	Neomorphosed, no sheet preservation
C. fallax Contejean	Jurassic (Kimmeridgian)	Market Rasen, UK, SM X.24507	Neomorphosed, no sheet preservation
C. hulliana Morris	Jurassic (Forest Marble)	Kirtlington, UK, SM X.24506	Neomorphosed, no sheet preservation
Jurassicorbula edwardi (Sharpe)	Jurassic (Kimmeridgian)	Santa Cruz, Portugal, SM X.24505	Well preserved microstructure but no sign of sheets
J. edwardi	Jurassic (Kimmeridgian)	Praia Areia Branca, Portugal, SM X.24504	Well preserved microstructure but no sign of sheets

Appearance of the conchiolin sheets in fossil corbulids

Direct microstructural evidence. With good preservation it is possible to recognize the presence of conchiolin sheets, but this is not true for specimens in which the aragonite has been replaced by either drusy calcite or silica. In some cut specimens, the MCL (at least) is visible to the naked eye as a dark brown line within the shell (e.g. Eocene *Corbula ficus* SM X.24517*b*) but in the majority of specimens it was only identifiable by SEM. Care must be taken not to confuse possible conchiolin sheets with myostracal layers. The latter are distinguishable by their prismatic structure and more curved trajectories, which terminate at the pallial and adductor muscle scars. Conchiolin sheets are in contrast frequently amorphous or sometimes granular, often of varying width, and coalesce with one another. Table 3 records the results of the SEM survey and Plate 1 displays some of the evidence for preserved conchiolin sheets. In Tertiary material at least, one sheet (the MCL) was clear and in some species (e.g. Miocene *Corbula carinata* and *C. alabamiensis*) there are multiple sheets. Sheets were less easy to recognize in *C. gibba* and no sign of their presence was found in Oligocene *C. vectensis*. X-ray micro-analysis of the sheets in Eocene *C. ficus* reveals that they are preserved in calcium carbonate but have an iron signature not found in the crossed lamellar aragonite on either side of the MCL. The oldest conchiolin sheets were noted in Maastrictian *C. crassiplica* (Pl. 1, fig. 6). Unfortunately, early Cretaceous *C. elegans* and *C. truncata* from the Blackdown Greensand, as noted by Taylor *et al.* (1983), were silicified with no relict microstructure, but other early Cretaceous specimens of *C. gaultina* and *C. striatula* did have preserved microstructure but had no sign of conchiolin sheets. Most Jurassic specimens lacked original mineralogy and structure, but some specimens of *Jurassicorbula edwardsii* collected by Fürsich and Werner from the Kimmeridgian of Portugal show fine preservation of the aragonite microstructure, but again no sign of conchiolin sheets.

Indirect methods. Species, in which the presence of conchiolin sheets may be inferred from the presence of an internal furrow or by taphonomic splitting, are marked accordingly in Appendix 1. For all Tertiary and Late Cretaceous taxa for which a significant number of specimens were examined, conchiolin sheets were suggested by one or, more often, both indicators, providing strong evidence for the presence of the MCL. Many Early Cretaceous specimens were furrowed, as was noted by Lewy and Samtleben (1979) for *Corbula elegans*, but, despite examination of 854 individuals, no positive sign of taphonomic splitting was apparent. There was no evidence of either indicator from the Jurassic.

INTERPRETATIONS

The results from each of the three approaches have been interpreted as follows.

Borehole survey

Recent levels of gastropod predation on corbulids were reached by the Late Cretaceous, very early in the history of boring. These findings agree with the previous studies of de Cauwer (1985) and Allmon *et al.* (1990), but not those of Kelley and Hansen (1993) who found that boring frequency remained low throughout the Cretaceous, rising sharply at the K-T boundary. Likelihood of borehole failure has not increased significantly over geological time.

Geographical distribution of conchiolin sheets

There is no evidence that corbulids which inhabit colder waters have better developed conchiolin sheets as an adaptation against shell dissolution. Although some high latitude taxa do have numerous and thick sheets, there is no statistically significant equatorward increase in their development.

Temporal distribution

Amalgamating both the direct and indirect evidence, it is clear that conchiolin sheets in corbulids were not present in the Jurassic but had become well developed by the Late Cretaceous. Evidence for the conchiolin sheet in Early Cretaceous corbulids is equivocal, restricted to inference from the furrowed right valve. As noted earlier, this is the weakest criterion for recognition of the MCL and, in isolation, cannot be taken as positive indication of its presence. It is probable that, in these taxa, thin conchiolin sheets were present but that they were not thick enough either to be detected by SEM or to cause taphonomic splitting. Selection pressures favouring the evolution of conchiolin sheets, as an adaptation to retard shell dissolution and non-predatory borers and to prevent crack propagation, have been operational since at least the early Mesozoic with no increase in intensity at the beginning of the Cretaceous. However, pressure to acquire defences from predatory borers rose sharply at that time. The first well developed MCL coincides with this increase in predation pressure and it is thus suggested that conchiolin sheets evolved as a primary adaptation to that threat. It is likely that earlier corbulids did possess some vestiges of organic layers in their shells but these are not uncommon in other bivalves (personal observation) and it is unlikely that such thin sheets could have provided an effective barrier against borers or dissolution. Once acquired, however, well developed conchiolin sheets would have had additional value in these other ways. They may also have had a profound effect on the evolution of corbulid overall morphology by allowing the valves to become grossly discordant. Coincidence of the MCL with the furrow into which the left valve fits, greatly facilitates the hermetic seal during adduction (Lewy and Samtleben 1979). Early corbulids (prior to the appearance of the MCL) are notably less inequivalve and less discordant than their descendants. Vermeij (1987) regarded discordance in bivalves itself as a defensive adaptation, providing a wide expanse of valve margin which may be damaged without harming the hermetic seal. However, Yonge (1946) observed that this grossly inequivalve shape has contributed to the poor burrowing ability of these bivalves and hence has precluded escape as an effective defence.

It might be expected that early gastropod borers were inefficient predators and the high rate of failure sustained in the Cretaceous reflects this, but that later failures were due to enhanced prey defences. However, as noted by Taylor *et al.* (1983), the earliest known Albian borings already reveal well established predatory behaviours, such as preference for the right valve. Failure rate has remained relatively constant over geological time and so any 'improvement' in corbulid defence must have occurred as part of an 'arms race' in tandem with increased predator efficiency rather than by the sudden evolution of a wonder trait.

DISCUSSION

In the evolution of prey taxa, predation failure is an important process; high failure rates in species which display variability in their defences is likely to lead to selection of anti-predatory traits (Vermeij 1982). With particular reference to boring predation, Vermeij suggested that naticid gastropods seldom fail to complete their attack once they have seized their prey, and therefore the

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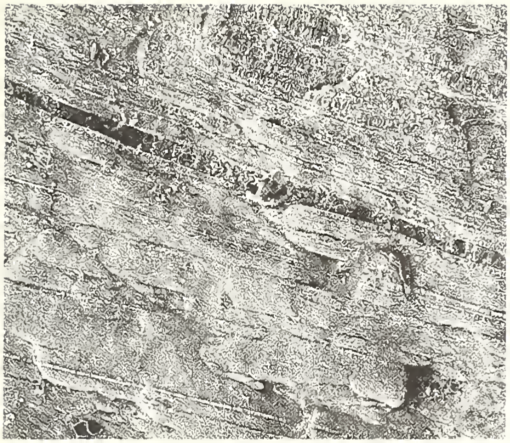
EXPLANATION OF PLATE 1

Figs 1–6. Preservation of conchiolin sheets in fossil corbulids. 1, *Corbula gibba* (Olivi); SM X.24529; Holocene; shell banks, Westerschelde, Holland; ×250. 2, *C. carinata* Dujardin; SM X.24524; Miocene; Bordeaux, France; ×80. 3, *C. ficus* (Solander); SM X.24517; Barton Beds, Eocene; Barton, UK; ×800. 4, *C. murchisoniana* Lea; SM X.24516; Claiborne Formation, Eocene; Alabama, USA; ×230. 5, *C. alabamiensis* Lea; SM X.24520; Claiborne Formation, Eocene; Alabama, USA; ×900. 6, *C. crassiplica* (Gabb); SM X.24527; Maastrichtian; Georgia, USA; ×130.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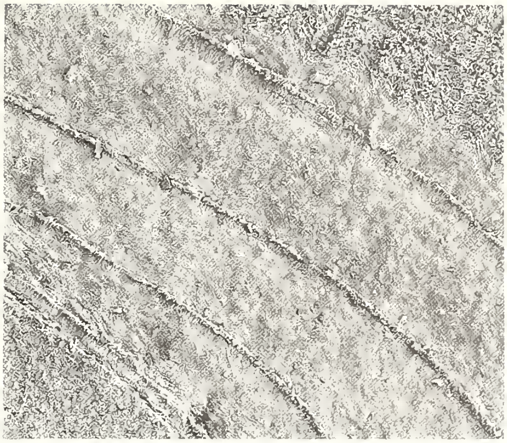
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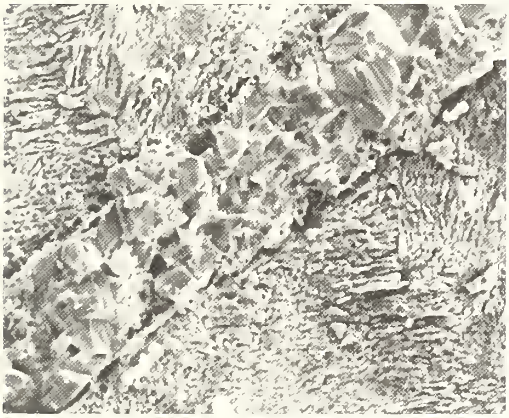
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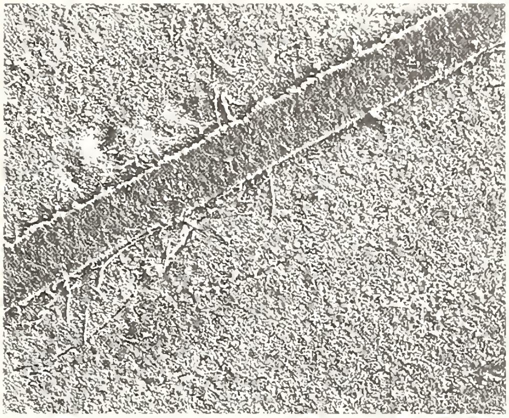
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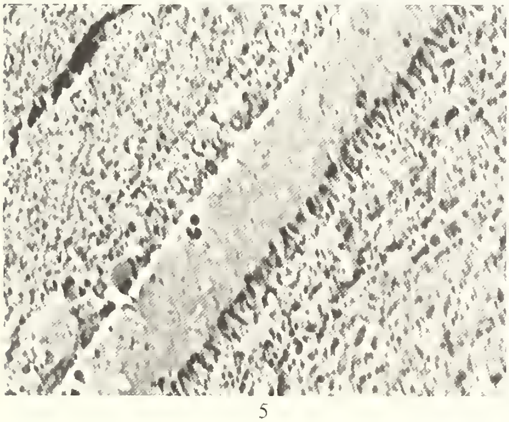
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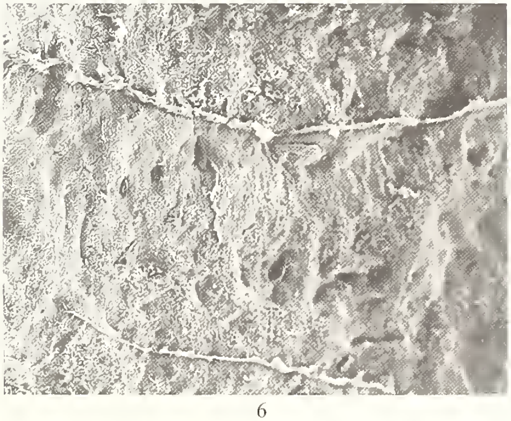
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HARPER, corbulid conchiolin sheets

chief line of defence against these predators is evasion of detection and of engulfment by the gastropod foot. Being slow burrowers, however, corbulids cannot escape and thus must rely on passive constructional defences, which retard the boring process to make them unprofitable prey. As de Cauwer (1985) pointed out, the high number of failed boreholes in corbulids attests not only to their success in foiling predation attempts but also to their initial vulnerability to attack (although it may also reflect longevity). But are corbulids really more resistant to attack than most other bivalves and how important are conchiolin sheets in their defence?

Vermeij (1987) and Vermeij *et al.* (1989) calculated the proportion of boring attempts that end in failure, and used this as an index of the effectiveness of the prey's defences. There are several flaws to this approach when applied to small sample sizes; failure may be related to factors other than prey defence (e.g. changing environmental conditions and predation or competition affecting the would-be predator itself) and it takes no account of attacks terminated before their traces are readily detectable to the investigator. Nevertheless corbulids do tend to show high values for this parameter. Vermeij (1987, table 11.5) provided data for the proportions of failed boreholes in a number of infaunal bivalves of Plio-Pleistocene, Miocene and Eocene age. In order to ascertain whether corbulids of the same ages were more or less susceptible to successful predation, the data in Table 1 were compared with Vermeij's non-corbulid data using the Permutation Test. Significantly higher failure rates in corbulids were discovered for the Miocene and Eocene (both at the five per cent level) but not for the Plio-Pleistocene. Although Morton (1990) considered that *Corbula crassa* is 'virtually immune from gastropod predation' in Tolo Channel, his study was restricted to live individuals which had evaded death and he did not record the incidence of complete boreholes in empty shells. Conchiolin sheets do not confer complete defence; sixty five per cent of all boreholes in the current survey were successful.

Conchiolin sheets may not be the only means by which corbulids gain defence. Possession of (i) a thickened periostracum and (ii) thickened valves may also slow boring and therefore promote failure.

Corbulids do possess thick periostraca; values of over 100 μm have been recorded for both *Corbula gibba* and *C. crassa* (Harper, unpublished data). I have found no evidence for the periostracum being thicker on the left valve than on the right, as suggested by de Cauwer (1985), although that of the right was often more abraded, particularly on the older part of the shell. This latter observation might explain the frequently expressed preference for boring the right valve.

Kelley (1989) reported that in the Miocene *C. idonea* there was an eight per cent increase in thickness over a three million year period, which she attributed to predation pressure. Crossed and complex crossed lamellar aragonite microstructures have a low organic content (Taylor and Layman 1972) and are thus metabolically cheap and rapid to lay down (Gabriel 1981), ideal for thick shells. These microstructures also fared well against Gabriel's simulated ABO attack, despite their low organic content. However, the case for increased shell thickness as a defence against boring predators, although appealing, is far from proven. Stereotyped borehole positioning in the umbonal region means that the borers often select the thicker part of the shell (Harper and Skelton 1993*b*), and Kabat (1990) noted that naticids have no known mechanism for gauging prey thickness. Boggs *et al.* (1984) experimentally showed that the naticid *Polinices* was unable to detect and select *Mercenaria* with artificially thinned valves.

In recent years there has been much debate over whether naticid predation of corbulids occurs less frequently and less predictably than suggested by the models of Kitchell *et al.* (1981), whether attacks fail more often than with other prey and what role the conchiolin sheets play in these anomalies (Kitchell *et al.* 1986; Kelley 1988, 1989; Anderson *et al.* 1991; Anderson 1992). It seems unnecessary to consider anomalous predation patterns and high failure rate together; the two need not be related. Given the interest in corbulid predation, there is a surprising lack of experimental information on how long it takes various gastropods to detect, bore and consume corbulid prey, and no assessment of the energy yield gained from these prey. Does the amount of energy gained from consuming a corbulid outweigh difficulties in detection and boring? Additionally, previous studies on muricids boring bivalve prey have shown that stereotypic predatory behaviour results from experienced individual predators and that inexperienced individuals do not feed in a predictable pattern (Hughes and Dunkin 1984); the possibility of experience being equally important for naticids needs to be addressed.

The presence of conchiolin sheets may affect some aspects of predation but not others. Although conchiolin sheets do cause a high failure rate, they are unlikely to explain the non-stereotypic borehole positioning reported by Kelley (1988). The morphology of the failed boreholes studied suggests that most terminate at the MCL. Since the MCL covers the entire valve, there is no advantage to boring at random locations in order to try and avoid conchiolin patches.

A frequent objection to assigning defensive value to conchiolin sheets is that failure rate is often highly variable (Anderson *et al.* 1991; Anderson 1992). Although in this survey failure rate was zero to eighty five per cent, zero failures were recorded in only two taxa (*Corbula elegans* in which Taylor *et al.* (1983) do record high failure rates, and *C. vectensis* which has very thin valves) and in the remaining species failure was more common. Another reason why Anderson (1992) rejected the importance of conchiolin sheets is that anomalous predation is also found in bivalve taxa which lack them. Harper and Skelton (1993*a*) demonstrated a range of means by which bivalves are known to gain defence from the attentions of boring gastropods (shell microstructure, periostracal fabric, valve thickness, valve ornament, behavioural modification, acquired toxicity, camouflage and active escape). Possession of conchiolin sheets is just one possibility; various bodyplan constraints prevent some clades from evolving some defensive adaptations but preadapts them for others. Not all infaunal bivalves are predapted for this particular defensive strategy.

Function of conchiolin sheets in other bivalve taxa

Well developed conchiolin sheets have been acquired independently in other bivalves but there is no requirement that they too should also have evolved in response to predation pressure. It is most unlikely that borers (either predators or endoliths) were responsible for their evolution in the unionoids. In his review of borers, Kabat (1990) documented few examples in freshwater habitats. It is more likely here that the sheets are a protective adaptation against shell dissolution, as suggested by Tevesz and Carter (1980), Kat (1983) and Isaji (1993).

A survey of Recent genera has revealed conchiolin sheets in some species of the ostreid genera *Alectryonella*, *Crassostrea*, *Ostrea*, *Saccostrea* and *Striostrea* as well as the gryphaeids *Hyotissa* and *Neopycnodonte*, although they are frequently less well developed than those reported in *Saccostrea cucullata* (Taylor 1990). It is unclear whether conchiolin sheets are a synapomorphic character of the Ostreoidea (in which case we might expect them to be apparent by the Jurassic) or whether they were independently acquired in the Ostreidae and Gryphaeidae (in which case they would appear later and probably at separate times). What is the primary function of these sheets in oysters? Taylor (1990) demonstrated that the sheets in *Saccostrea cucullata* provided defence against boring muricid gastropods, whilst Korringa (1951) suggested their function in *Ostrea edulis* was to deter polydorid polychaete borings. According to Hudson and Palmer (1976), significant moments in oyster evolution occurred in euryhaline habitats, where selection pressure to acquire conchiolin sheets to prevent shell dissolution would have been high. Resolution of these questions could be achieved by conducting a study similar to that above. This should be easier than for corbulids, as oysters are predominantly composed of calcite rather than aragonite so there is no loss of information due to diagenetic dissolution and recrystallization. Positive identification of conchiolin sheets may be hampered, however, by the fact that many oyster shells contain fluid filled chambers and chalky layers (Korringa 1951), and there appears to be no morphological expression of the sheets such as the furrow in corbulids. If these problems can be overcome such a study may prove fruitful.

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APPENDIX 1

Raw data on boring frequencies and stratigraphical information for the corbulids studied. [F] and [T] indicate species in which an internal furrow, and taphonomic splitting, respectively, have been observed. Information in round brackets refers to valve preference; X = no preference, R = preference for the right valve where $P > 0\cdot05$, * = $P < 0\cdot05$, ** = $P < 0\cdot0$ and *** = $P < 0\cdot001$.

Species	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
Jurassic					
C. attenuata Lycett	Forest Marble, Minchinhampton, UK	101	0	—	—
C. bayani de Loriol	Portland Clay, Swindon, UK	10	0	—	—
C. buckmani Lycett	Great. Oolite, Minchinhampton, UK	26	0	—	—
C. chilmarkensis Cox	Portland Oolite, Portland, UK	18	0	—	—
C. deshayesea Skeat	Jutland, Denmark	9	0	—	—
C. fallax Contejean	Kimmeridge Clay, Market Rasen, UK	32	0	—	—
C. hulliana Morris	Great Oolite, Kirtlington, UK	29	0	—	—
C. involuta Münster	Forest Marble, Laycock, UK	2	0	—	—
C. islipiensis Lycett	Forest Marble, Laycock, UK	1	0	—	—
C. lyrata Sowerby	Kutch, India	6	0	—	—
C. macneilli Morris	Oxford Clay, Studley, UK	26	0	—	—
C. pectinata Sowerby	Kutch, India	50	0	—	—
C. sp.	Various	26	0	—	—
Corbulomima suprajurensis (d'Orbigny)	Kimmeridgian, Santa Cruz, Portugal	2	0	—	—

Species	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
Jurassicorbula edwardii (Sharpe)	Kimmeridgian, Santa Cruz, Portugal	4	0	—	—

Also examined: blocks of *C. hebredica* Tate (Great Estuarine Group) and *C. alata* Sowerby (Purbeck Beds, Swanage, UK)

Species	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
Cretaceous					
C. angulata (Phillips)	Neocomian, Speeton Clay, Speeton, UK	50	0	—	—
C. elegans Sowerby [F]	Albian, Blackdown, UK	667	18(R***)	18	0
C. gaultina Pictet and Campiche	Gault, Folkstone, UK	7	0	—	—
C. striatula Sowerby [F]	Aptian, Lower Greensand, Atherfield, UK	127	0	—	—
C. truncata [F]	Albian, Blackdown, UK	53	9(X)	3	6
C. truncata	Cenomanian, Dunscombe and Chard, UK	4	0	—	—

Also examined: *C. crassiplica* (Gabb) [F, T] (Coon Creek, Washington, Maastrichtian); *C.* sp [F, T] (Gosau, Upper Cretaceous) and *C. truncata* [F] (Bracquegriues, Belgium, Albian).

Species	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
Paleocene					
C. regulbiensis Morris [F, T]	Thanet Sands, Herne Bay, Kent, UK	592	77(X)	37	40
Eocene					
C. alabamiensis Lea [F, T]	Claiborne Formation, Alabama, USA	231	31(R*)	13	18
C. aldrichi Meyer [F, T]	Woods Bluff, Alabama, USA	29	6(R*)	4	2
C. ampullacea (Deshayes)	Paris Basin, Grignon, France	1	0	—	—
C. anantina (Lamarck)	Paris Basin, Grignon, France	3	0	—	—
C. arnouldi Woods	Negritos, Peru	54	1	1	0
C. angulata (Lamarck)	Paris Basin, Grignon, France	5	0	—	—
C. bicarinata Conrad	Mississippi, USA	14	0	—	—
C. costata (Sowerby) [F, T]	Barton Clay, Barton, UK	27	13(R*)	2	11
C. cuspidata Sowerby [F, T]	London Clay, Portsmouth, UK	11	0	0	0
C. cuspidata [F, T]	Bracklesham Beds, Barton, UK	21	3	2	1
C. cuspidata [F, T]	Barton Clay, Hampshire, UK	169	15(X)	12	3
C. cuspidata [F, T]	Headon Beds, Hampshire, UK	140	21(X)	17	4
C. densata Conrad	Mississippi, USA	4	0	—	—
C. exarata (Deshayes)	Paris Basin, France	1	0	—	—
C. ficus (Solander) [F, T]	Barton Clay, Barton, UK	44	4	1	3
C. gallica (Lamarck)	Paris Basin, Grignon, France	15	0	—	—
C. gallica	Barton Beds, Barton, UK	27	0	—	—
C. lamarckii Deshayes	Barton Beds, Bunny Beacon, UK	7	0	—	—
C. longirostris Deshayes [F, T]	Barton Beds, Barton, UK	31	1	1	0
C. murchinsonia Lea [F, T]	Claiborne, Alabama, USA	119	17(R**)	8	9
C. nastua Conrad [F, T]	Claiborne, Alabama, USA	13	3	1	2
C. nitida Sowerby [F, T]	Headen Beds, Brockenhurst UK	6	1	1	0
C. oniscus Conrad [F]	Claiborne, Alabama, USA	45	2	2	0

Species	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
C. peruviana Woods	Negritos, Peru	54	1	0	0
C. pisum Sowerby [F]	London Clay, Portsmouth, UK	182	8	6	2
C. pisum [F]	Headon Beds, Hampshire, UK	15	2	2	0
C. pisum [F]	Barton Beds, Barton, UK	664	74(R***)	64	10
C. pisum [F]	Headon Beds, Hampshire, UK	394	17(R*)	10	7
C. revoluta (Brocchi) [F]	Barton Beds, Barton, UK	45	4	3	1
C. striata Deshayes [F]	Bracklesham Beds, Barton, UK	18	0	—	—
C. striata [F]	Barton Clay, Barton, UK	47	3	2	1
C. waringi Woods	Negritos, Peru	8	0	—	—
Oligocene					
C. alta Conrad	Vicksburg, Mississippi, USA	7	0	—	—
C. descendens Forbes [F]	Isle of Wight, UK	42	0	—	—
C. engonata Conrad	Vicksburg, Mississippi, USA	13	0	—	—
C. gibba (Olivi) [F]	Berg, Belgium	42	1	0	1
C. gibba [F]	Isle of Wight, UK	42	0	—	—
C. laqueata Conrad [F, T]	Vicksburg, Mississippi, USA	27	1	1	0
C. pisum Sowerby	Isle of Wight, UK	11	0	—	—
C. rotunda Sowerby	Kassel, Germany	2	0	—	—
C. rugosa Lamarck	Kassel, Germany	5	0	—	—
C. subpisum Sowerby	Isle of Wight, UK	10	1	1	0
C. vectensis Forbes [F, T]	Isle of Wight, UK	497	11(X)	11	0
Miocene					
C. canaliculata Hutton [F, T]	Canterbury, New Zealand	4	1	1	0
C. carinata Dujardin [F, T]	Bordeaux, France	387	32(X)	21	11
C. elevata Conrad	Maryland, USA	6	0	—	—
C. funiakensis Gardner	Chipola Formation, Florida, USA	6	1	0	1
C. gibba (Olivi) [F, T]	Gironde, France	416	91	59	32
C. heterogena Dall	Bowden, Jamaica	5	0	—	—
C. idonea Conrad [F, T]	Chesapeake Group, Maryland, USA	8	2	0	2
C. radiatula Dall [F]	Chipola Formation, Florida, USA	10	2	1	1
C. revoluta (Brocchi) [F, T]	Ponteleroy, France	41	3	1	0
C. seminella Dall	Chipola Formation, Florida, USA	13	1	1	0
C. sericea (Dall) [F, T]	Bowden, Jamaica	45	15	10	5
C. waltonensis Dall	Chipola Formation, Florida, USA	6	0	—	—
Pliocene					
c. gibba (Olivi) [F, T]	Coralline Crag, Suffolk, UK	15	0	—	—
C. gibba [F, T]	Antwerp, Belgium	91	0	—	—
C. gibba [F, T]	Nicosia, Cyprus	106	0	—	—
C. gibba [F, T]	Piedmont, Italy	282	20(X)	12	8
C. inaequalis Say [F, T]	South Carolina, USA	76	13(X)	10	3
C. macilenta Hutton [F, T]	Wanganui, New Zealand	4	1	1	0

Species	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
C. revoluta (Brocchi) [F]	Piedmont, Italy	3	0	—	—
C. rotundata Sowerby	Anvers, Belgium	6	0	—	—
C. sp.	Various	12	0	—	—
C. striata Walker and Boys [F, T]	Coralline Crag, Suffolk, UK	148	8	5	0
C. striata [F, T]	Piedmont, Italy	48	6	1	5
Pleistocene					
C. gibba (Olivi) [F, T]	Red Crag, Suffolk, UK	46	0	—	—
C. gibba [F, T]	Weybourne Crag, Suffolk, UK	43	2	2	0
C. striata Walker and Boys	Red Crag, Suffolk, UK	23	3	2	1

APPENDIX 2

Data from previously published works. 1, Taylor *et al.* (1983); 2, de Cauwer (1985); 3, Speden (1970); 4, Taylor (1970); 5, Adegoke and Tevesz (1974); 6, Arua (1989); 7, Kelley (1989); 8, Hoffman *et al.* (1974); 9, Robba and Ostinelli (1975); 10, Anderson *et al.* (1991).

Species	Author	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
Cretaceous						
Corbula elegans Sowerby	1	Albian, Blackdown Greensand, UK	712	42	?	?
C. truncata Sowerby	1	Albian, Blackdown Greensand, UK	145	7	?	?
C. crassiplica (Gabb)	2	Campanian, Coon Creek, Tennessee, USA	294	57	48	9
C. crassiplica	2	Campanian, Mercers Mill, Georgia, USA	331	96	74	22
C. substriatula d'Orbigny	2	Campanian, Vaals, The Netherlands	484	99	70	29
Corbulamella gregarea Meek and Hayden	3	Maastrichtian, Fox Hills Formation, South Dakota, USA	332	115	?	?
Eocene						
Bicorbula gallica (Lamarck)	4	Lutetian, Damery, France	27	5	?	?
C. brabantina Vincent	2	Lutetian, Oedelem, Belgium	315	139	131	8
C. rugosa Lamarck	4	Lutetian, Damery, France	179	27	?	?
C. rugosa	2	Lutetian, Grignon, France	524	146	121	25
C. rugosa	2	Lutetian, Parnes, France	578	128	104	24
V. amekiensis (Eames)	5	Lutetian, Ameki Formation, Nigeria	89	28	25	3
V. amekiensis	6	Lutetian, Ameki Formation, Nigeria	403	20	?	?
Miocene						
C. idonea Conrad	7	Chesapeake Group, Maryland, USA	361	20	?	?
C. gibba (Olivi)	8	Korytnica Clays, Poland	928	251	?	?
C. gibba	2	Mellesdorf, Austria	443	90	87	3

Species	Author	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
Plio/Pleistocene						
C. gibba	9	Italy	804	126	?	?
Varicorbula caloosae (Dall)	10	Sarasota, USA	?	43	38	5
V. caloosae	10	Davis, USA	?	42	39	3
V. caloosae	10	Forsberg, USA	?	29	28	1
V. caloosae	10	Punta Gorda, USA	?	31	27	4

AUSTRALOSYODON, THE FIRST PRIMITIVE ANTEOSAURID DINOCEPHALIAN FROM THE UPPER PERMIAN OF GONDWANA

by BRUCE S. RUBIDGE

ABSTRACT. A new genus and species of anteosaurid dinocephalian, *Australosyodon nyaphuli*, is described from the *Eodicynodon–Tapinocaninus* Assemblage Zone, the lowermost biozone of the Beaufort Group in South Africa. This genus, closely allied to *Syodon*, is the first undoubted primitive anteosaurid dinocephalian from outside Russia, and indicates that the earliest therapsids were also present in the southern hemisphere.

DINOCEPHALIANS formed part of the earliest therapsid fauna of the Russian Ocher and Isheevo formations (Tchudinov 1965) and one genus has been described from the San Angelo Formation of Texas (Olson 1962). They were also present as an important part of the therapsid fauna of the Beaufort Group of South Africa (Boonstra 1969; 1971; Keyser and Smith 1978; Rubidge 1991).

The most primitive dinocephalians have been thought to be the Russian Anteosauridae (Boonstra 1971; Hopson and Barghusen 1986), although some palaeontologists consider the Estemmenosuchidae to be the least derived group (Kemp 1982; King 1988). Anteosaurid dinocephalians are found together with the earliest known therapsids in the Russian Ocher Complex (Zone I) (Tchudinov 1960; 1983), and there is a series of fragments referred to as *Eosyodon* from the San Angelo Formation of Texas (Olson 1962) (although Parrish *et al.* (1986) questioned the identification of the latter as therapsids). However, the group is far better represented in the younger rocks of the Russian Isheevo Complex (Zone II) (Orlov 1958). Until now, the only anteosaurid from Gondwana has been the very derived genus *Anteosaurus* from the Dinocephalian Assemblage Zone of South Africa. The skull of a carnivorous dinocephalian recently collected from the underlying *Eodicynodon–Tapinocaninus* Assemblage Zone is much more primitive than *Anteosaurus*, instead resembling the most primitive anteosaurids of the Russian fauna.

MATERIAL AND METHODS

In 1987, Mr John Nyaphuli of the National Museum in Bloemfontein discovered a calcareous nodule which had shattered into several pieces, all of which contained fossilized bone. All but one of the missing fragments of the nodule were found, and stuck together prior to preparation, so that the present orientation of the bones is as they were when the skull was fossilized. Eighteen months later, on returning to the locality where the fossil was discovered, the remaining portion of the nodule was found. By this stage the rest of the skull had been prepared, and it proved difficult to be sure that the newly found piece of the nodule, containing the lateral flange of the pterygoid, was precisely correctly orientated.

Preparation was undertaken by Mr Nyaphuli using compressed air driven engravers. In areas requiring finer work, in particular, the separation of the intermeshing incisors of the upper and lower jaws, acid preparation was carried out using a ten per cent solution of acetic acid. Glyptal cement was used as adhesive and, on completion of preparation, the whole specimen was thinly coated with a dilute solution of Glyptal. The specimen (NMQR 3152) is housed in the Karoo fossil

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reptile collection of the National Museum, Bloemfontein, South Africa (Institutional abbreviation: NMQR).

The right side of the skull was badly crushed prior to fossilization, but the left side is relatively well-preserved and undistorted. A lower jaw is present and was tightly appressed to the upper jaw, prior to being removed by preparation.

SYSTEMATIC PALAEONTOLOGY

Subclass SYNAPSIDA Osborn, 1903
Order THERAPSIDA Broom, 1905
Infraorder DINOCEPHALIA Seeley, 1894
Family ANTEOSAURIDAE Boonstra, 1954
Genus AUSTRALOSYODON gen. nov.

Diagnosis. As for species.

Derivation of name. *Australo*, southern; *syodon*, the genus of anteosaurid dinocephalian most closely related to this specimen. The name refers to the first primitive anteosaurid from the southern hemisphere.

Australosyodon nyaphuli sp. nov.

Text-figures 1–8

Derivation of name. The species is in honour of John Nyaphuli who collected the specimen.

Diagnosis. Medium sized dinocephalian. Skull high and apparently narrow. Large frontal boss situated in interorbital region and extending anteriorly down the midline as a narrow interorbital ridge. Frontal bone forming anterior border of a depression for attachment of jaw adductor musculature which is present on skull roof lateral to pineal boss and immediately anterior to the temporal fenestra. In the palate, bosses on the palatines relatively large, protrude ventrally and bear at least twelve teeth which tend to be posteriorly inclined. Pterygoid teeth on median pterygoid boss, but absent on the lateral pterygoid flange. Dental formula i5/4 c1/1 pc12–13/7. Small incipient heel present on lingual side of lower incisors, but not manifestly present on upper incisors. Canines laterally flattened, having a sharp keel on the postero-medial edge. Postcanines relatively small, laterally compressed. Upper postcanines curve posteriad, lower postcanines point upwards with their tips pointing slightly posteriorly, and have small heels on the lingual side. Crowns of posteriormost postcanine of lower jaw antero-posteriorly broadened to form crushing surface.

Holotype. NMQR 3152. Skull and mandible, left side well preserved with several teeth; right side crushed prior to fossilization.

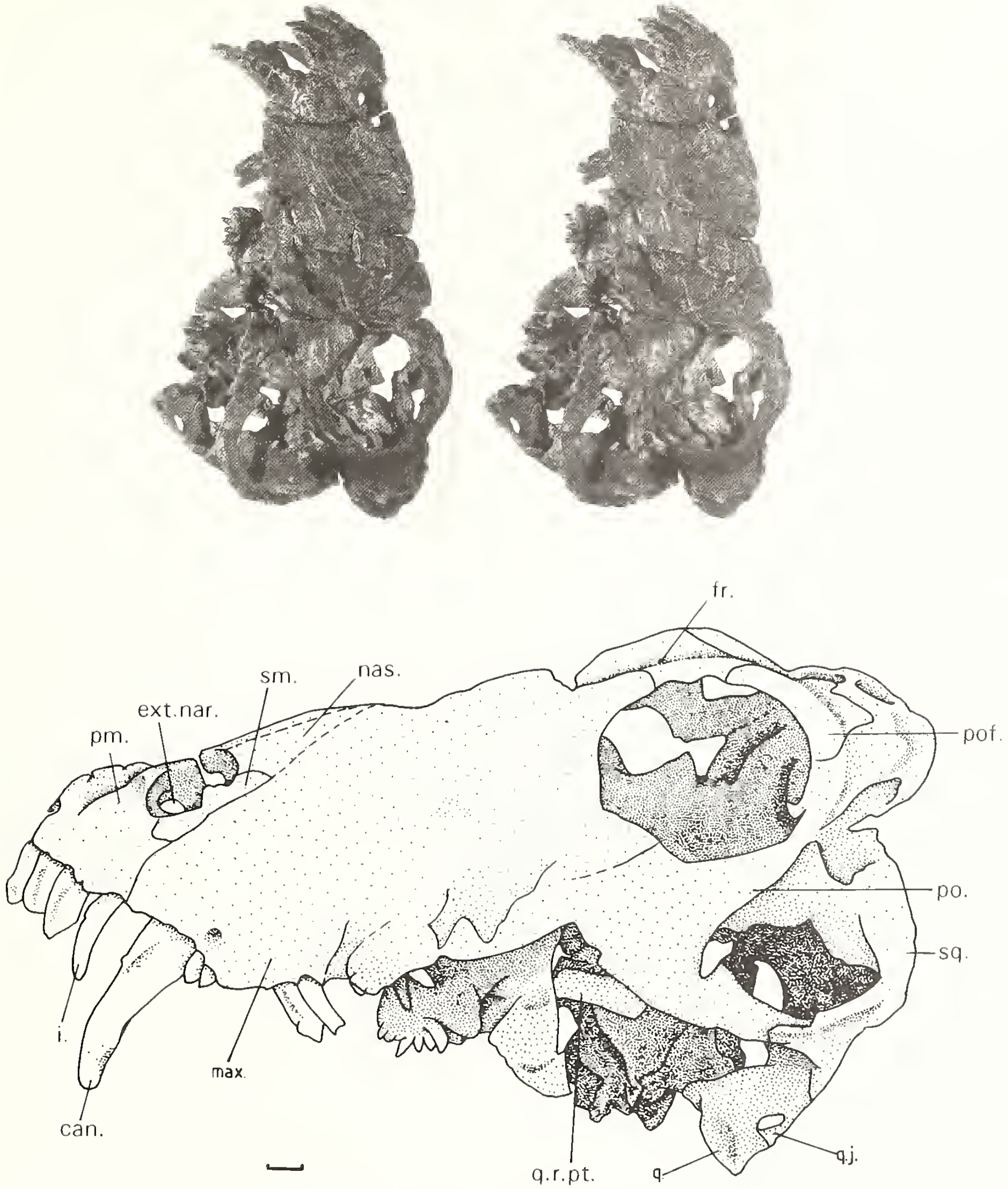
Type horizon and locality. *Eodicynodon–Tapinocaninus* Assemblage Zone at the base of the Beaufort Group on the farm Tuinkraal, Prince Albert Road, South Africa (map sheet: South Africa 1:50000, sheet 3321 BA Dwyka, first edition).

DESCRIPTION

The specimen, consisting of a skull and lower jaw, is more or less completely preserved. The right side has been crushed as a result of lateral compression and the zygomatic arch distorted in a medial direction resulting in the quadrate being displaced ventrally. The braincase and occiput have also been crushed.

Skull roof

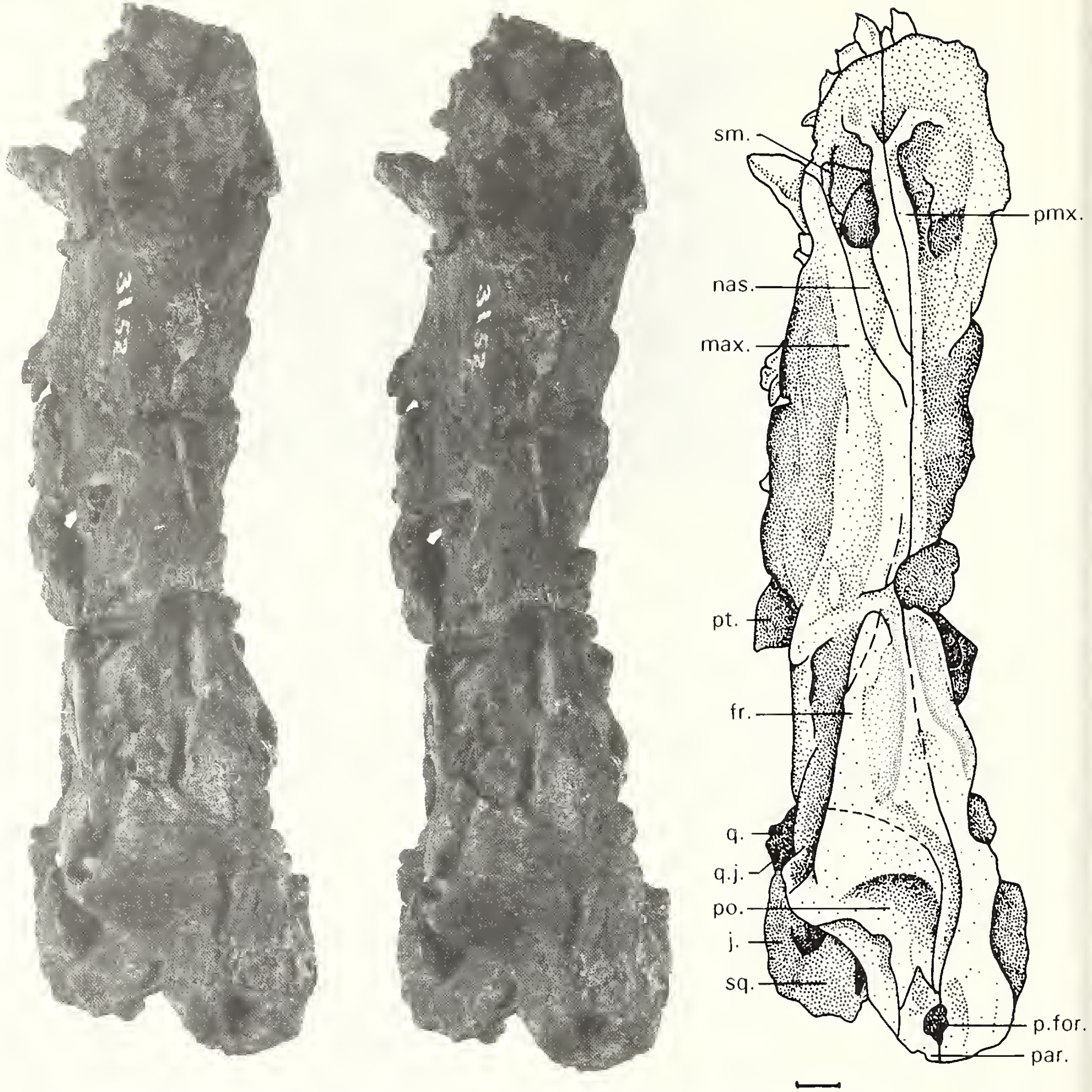
The premaxilla forms the anterior tip of the snout, and is well exposed on the lateral side of the skull (Text-fig. 1). Anterior to the canine the ventral edge of the premaxilla slopes anterodorsally. The premaxilla forms the anterior and dorsal borders of the external nares and thins as it extends postero-dorsally up the snout to



TEXT-FIG. 1. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of lateral view. Scale bar represents 10 mm.

form a wedge-shaped contact with the nasals. A vertically orientated suture extending from the antero-ventral end of the external nares to immediately anterior of the canine, forms the contact between the premaxilla and maxilla on the lateral side of the skull.

The septomaxilla forms the floor, and the ventral portion of the posterior border of the external nares. It also extends onto the lateral surface of the skull to meet the maxilla ventrally and posteriorly, and the nasals dorsally. Posteriorly it forms a pointed contact between the maxilla and nasal bones.



TEXT-FIG. 2. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of dorsal view. Scale bar represents 10 mm.

The maxilla forms most of the side of the snout. Dorsally it is in contact with the nasal, and appears to be in contact with the prefrontal posterodorsally, although the position of this suture is uncertain.

The anterodorsal border of the orbit is formed by the prefrontal which has been crushed on its anterior and ventral sides such that it is difficult to determine its relationship with the adjoining bones with certainty. Dorsomedially and posteriorly, the prefrontal is in contact with the frontal by means of a suture which extends anteromedially from the anterodorsal rim of the orbit at an angle of *c.* 45°. As this portion of the skull roof is weathered, it is not possible to determine the orientation of the sutures at the junction between the frontal, prefrontal and nasal bones. The sutures between the prefrontal and lachrymal bones are unclear, as also are those between the lachrymal, maxilla, and jugal.

The frontal forms a large portion of the dorsal border of the orbit. Because of the weathered nature of the skull roof anterior to the orbits, the contact between the frontal and nasal bones is unclear. From a point in line with the anterior margin of the orbit, a prominent longitudinal ridge extends posteriorly down the midline on the skull roof along the contact between the left and right frontal bones. Almost a quarter of the way along the frontal bone, this ridge flares laterally to form a boss on the skull roof above the posterior half of the orbit. Posteriorly, this boss slopes downwards gently, and continues as a longitudinal ridge which extends almost as far as the contact between the frontal and parietal bones (Text-fig. 2).

The suture forming the border between the frontal and postfrontal bones extends medially from the posterodorsal border of the orbit. Close to the midline, it curves in a posterior direction to meet the suture between the parietal and postorbital bones. The frontal thus continues posteriorly to form a narrow 'finger' between the postfrontal on the lateral side and the parietal medially. This narrow projection is not present in *Titanophoneus*, and in *Syodon* the author was not able to recognize the suture between the postorbital and postfrontal bones.

The sutural contact between the postfrontal and postorbital bones extends in a medial direction from the posterodorsal portion of the orbit. Close to the midline of the skull, the suture turns posteriorly towards the pineal foramen so that the postfrontal forms a pointed contact between the postorbital on the lateral side and the parietal on the posterior and posteromedial sides. This suture continues posteriorly on the dorsal portion of the zygomatic arch as the contact between the postorbital and parietal bones.

The parietal forms a narrow border around the anterior side of the pineal foramen. Anterolateral to the pineal foramen, this bone forms a wedge-shaped contact with the frontal; it meets the postfrontal anterolaterally, has a long sutural contact with the postorbital laterally and posterolaterally, and meets the tabular and interparietal on the posterior and posteromedial sides respectively (Text-fig. 2). The outer surface of the posterior region of the parietal is weathered but it appears to form a large proportion of the dorsal portion of the occipital plate on the posterior side of the skull.

The postorbital bone, which is not greatly pachyostosed, forms the entire posterior and posteroventral border of the orbit, as well as the dorsal border of the temporal fenestra. The suture between the postorbital and jugal bones on the posteroventral side of the orbit could not be determined.

The squamosal forms the posterodorsal and posterior borders of the temporal fenestra, and meets the jugal on the ventral margin of this opening. This contact is not clear. The skull is broken on the dorsal side of the temporal opening so that the contact between the postorbital, and squamosal is unclear. The jugal forms a portion of the ventral border of both the temporal fenestra and the orbit. The exact limits of this bone are uncertain as the sutures could not be determined.

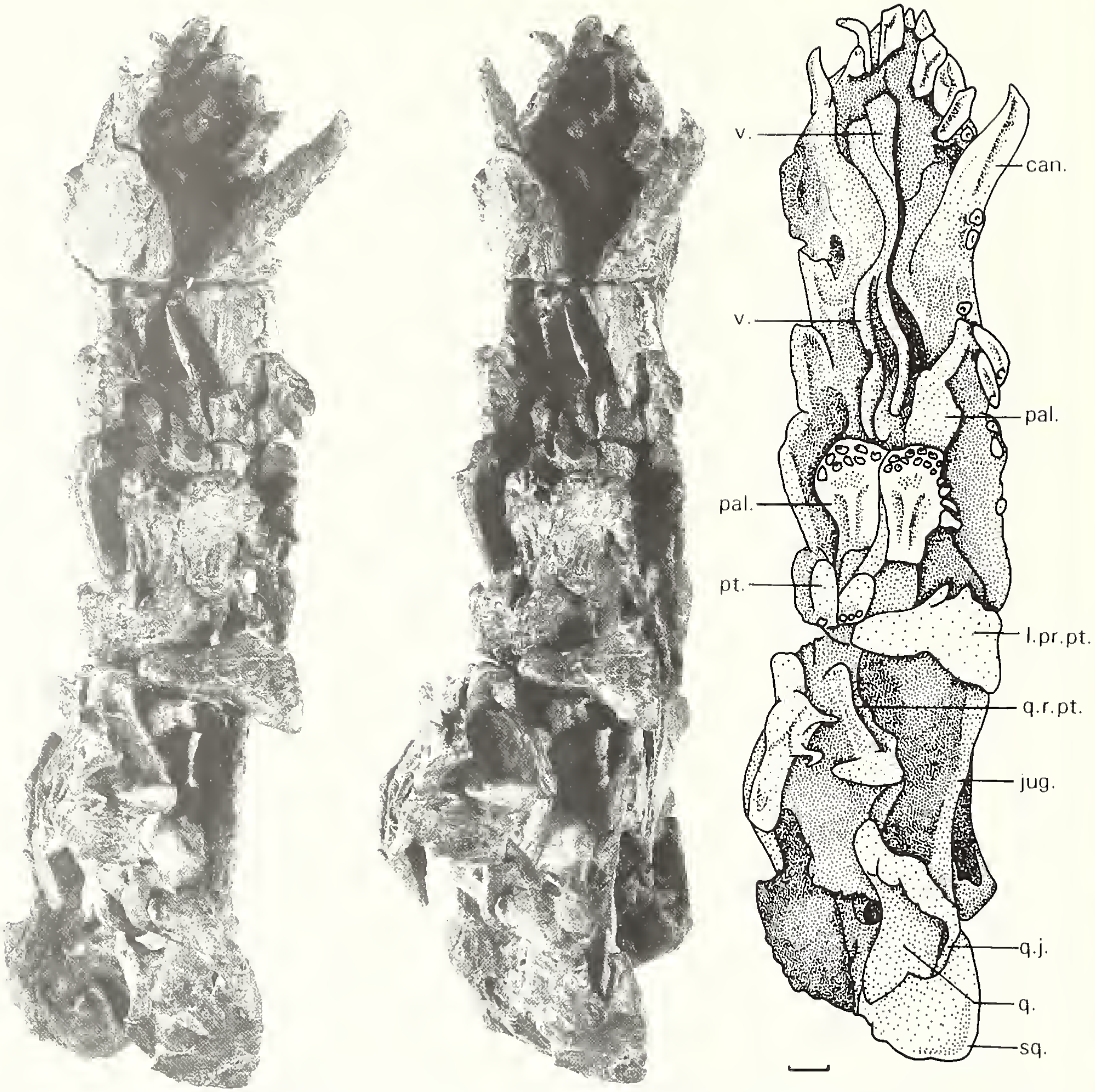
At the posterior end of the skull, the squamosal extends medially to form a plate-like bone, which meets the occipital bones on a ridge on the medial side. Dorsally it is in contact with the postorbital, and dorsomedially with the tabular. Ventrally the squamosal is in contact with the quadratojugal on the lateral side, and the quadrate on the medial side. The quadrate and quadratojugal overlie the squamosal on the anteroventral side.

The articulatory surface of the quadrate has two condyles, the medial one being smaller than the lateral one. When viewed from the posterior end, the quadrate is a broad bone which expands laterally and medially on the ventral side to form the articulatory condyles, and flares laterally on the dorsal side of the quadratojugal foramen so that the dorsal part of the bone is broad and fan-shaped. In lateral aspect, however, the quadrate is very narrow and plate-like. It is rounded on the posterior side and flattened anteriorly.

The quadratojugal is situated on the lateral side of the quadrate, and is a narrow bone when viewed from the anterior end. The ventral contact between the quadratojugal and the quadrate is situated immediately above the lateral articulatory condyle of the quadrate. The quadratojugal has an expansive footplate which extends in a medial direction beyond the limits of the quadrate foramen and overlies the posterodorsal side of the lateral quadrate articulatory condyle. On the lateral side of the foramen the quadratojugal is relatively narrow when viewed from the front but flares medially and laterally on the dorsal side of the quadratojugal foramen and here overlies the anterior side of the dorsal expansion of the quadrate.

Palate

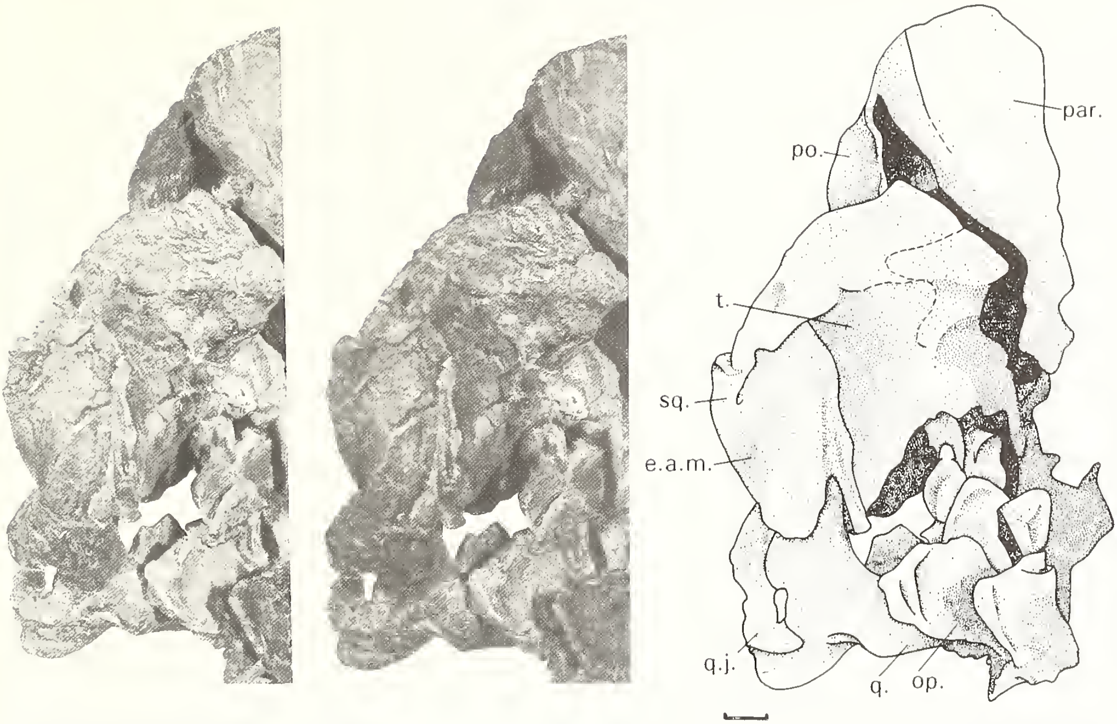
Posteriorly, the premaxilla is in sutural contact with the maxilla just in front of the canine tooth (Text-fig. 3). This suture continues medially immediately posterior to the recess in the upper jaw which accommodates the tip of the lower canine. From here the suture runs posteromedially to meet the border of the internal nares on the medial side of the canine. A longitudinal suture extends down the midline of the premaxilla.



TEXT-FIG. 3. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of ventral view. Scale bar represents 10 mm.

Five incisor teeth are present in each premaxilla. The first incisor is relatively small, the second is slightly larger and the third is the largest. The fourth incisor is the same size as the second, and the fifth is extremely small and is situated laterally to the recess in the premaxilla which serves to accommodate the tip of the canine of the lower jaw. As the crowns of most of the incisor teeth of the upper jaw are not preserved it is difficult to determine whether small heels were initially present on their lingual side. Immediately anteromedial to the canine, the premaxilla has an indentation which accommodates the canine of the lower jaw. The suture between the premaxilla and maxilla in the palate extends medially from between the canine and fifth incisor, to meet the antero-lateral border of the internal nares at a point in line with the posterior end of the canine.

The maxilla forms the lateral border of the internal nares and apart from a single canine; it also bears twelve to thirteen postcanine teeth. The canine, which is rounded on the lateral side and flattened on the medial side,



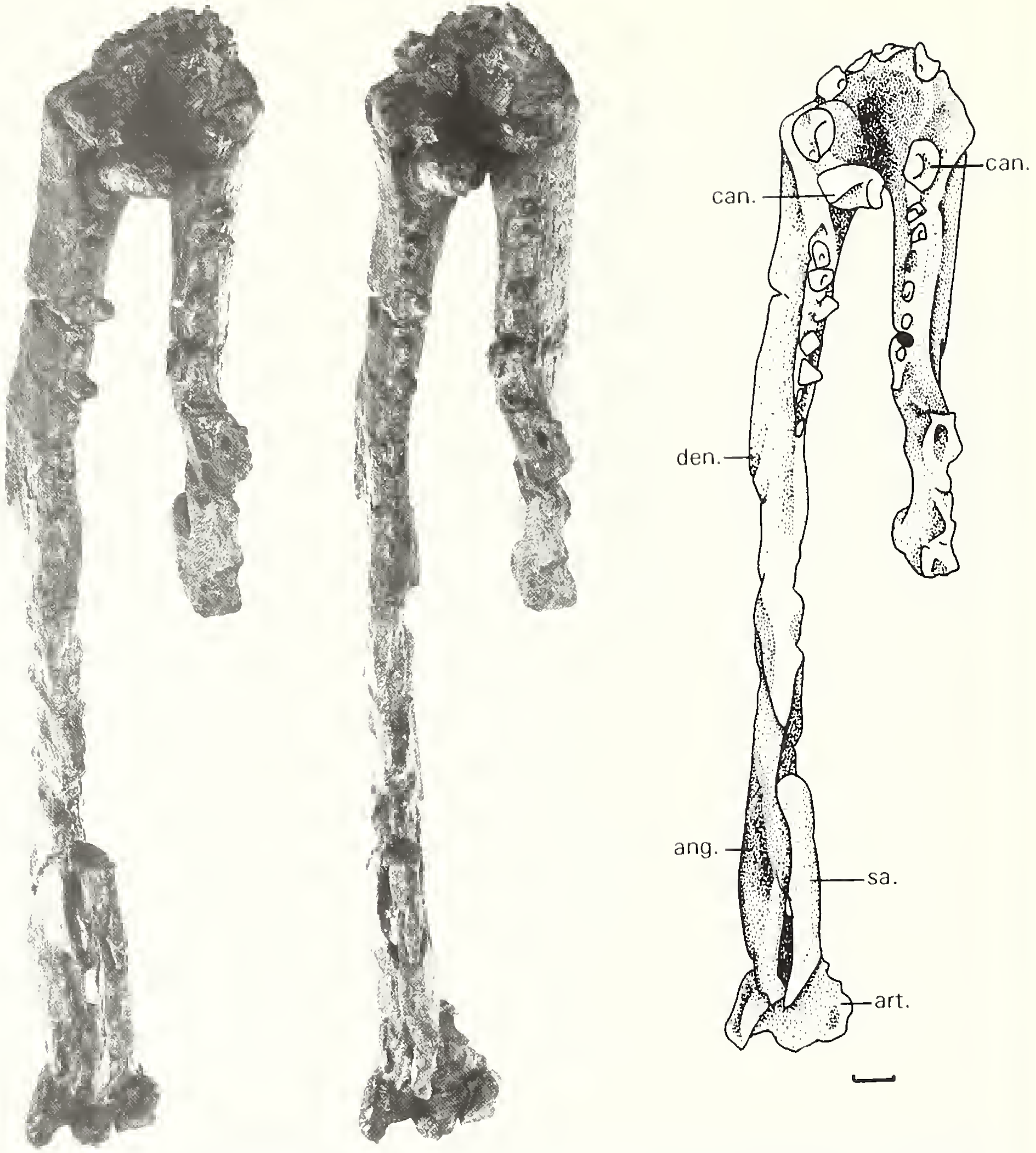
TEXT-FIG. 4. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of occipital view. Scale bar represents 10 mm.

has a slight keel on its posterior surface. It points slightly anteriorly and laterally in its proximal regions but, closer to the tip, it curves slightly in a posterior direction as well as curving medially.

The postcanines vary in shape and form, and apart from the first two postcanines, which point slightly anteriorly, the tips of the rest point in a posterior direction. The first postcanine is situated immediately posterior to the canine, and both the first and second postcanines are relatively short and blunt. Only the roots of postcanines 3, 4 and 5 are present, and the crowns of 6, 7 and 12 are preserved as well. Judging by the anterior-posterior diameter, postcanines 6 and 7 are the largest of the postcanine teeth. The posteriormost teeth are the smallest, being even smaller than the short and blunt anteriormost teeth. The crowns are rounded on the labial side, but flattened on the lingual side. In cross-section these teeth are slightly ovoid, being more rounded anteriorly and having a slight keel on the mesial side as in *Syodon*, except that in *Syodon* the teeth are not flattened on the lingual side. The postcanine teeth of *Australosyodon* are much more slender and gracile than those of *Syodon* and *Titanophoneus*. They differ further from those of both *Syodon* and *Titanophoneus* in that they are not faceted on the point and not rounded on the lingual side.

On its posteroventral side, the maxilla is overlain by an anterior projection of the palatine. The anterior end of this projection is not preserved on the left side, but the presence of a pointed groove which tapers forwards on the ventral surface of the maxilla, is evidence that this portion of the palatine once bordered the lateral margin of the internal naris. The left side of the palate has been crushed so that it is not possible to determine the extent of the anterior projection of the palatine on this side with certainty. Posteriorly, the palatine forms a prominent ventrally projecting boss which bears twelve to fourteen teeth arranged in two concentric semicircular rows.

The vomers are paired and extend posteriorly down the midline of the palate from the premaxilla anteriorly, to meet the palatines at the posterior end of the internal nares. From here the vomers taper medially to form a pointed contact between the palatine bosses. Because the palate was distorted prior to fossilization, the vomer has been buckled. It is evident, however, that the lateral edges of the vomer curved ventrally and medially to form a prominent, ventrally protruding ridge on the lateral side of the bone, as is in *Syodon*.



TEXT-FIG. 5. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of dorsal view of lower jaw. Scale bar represents 10 mm.

The relationship between the palatine and pterygoid is uncertain, as it appears that the palatine overlies the pterygoid on its anteroventral end. Posteromedial to the palatine boss, the pterygoid forms a smaller tooth-bearing ridge which is ovoid in shape with its pointed ends orientated anteroposteriorly. At least seven teeth are present on this ridge but their orientation cannot be determined as only the roots are preserved. A prominent ventrally projecting lateral flange of the pterygoid is present but, as the portion of the skull between the pterygoid bosses and the lateral flange of the pterygoid has been weathered away, it is not possible to determine the structure of this area of the skull. The quadrate ramus of the pterygoid flares posterolaterally at an angle of *c.* 30° to the midline. It is thin in ventral aspect, but broad when viewed laterally. The posterior half of the quadrate ramus has broken from the anterior portion and been medially displaced. As the quadrate has been ventrally displaced in the skull, as a result of distortion, it is not possible to determine the relationship between the quadrate ramus of the pterygoid and the quadrate.

The basisphenoid has been so severely crushed that its structure is indeterminable.

Occiput

Only the left side of the occiput is preserved and, by comparison with the skulls of *Syodon* and *Titanophoneus*, it appears that the occiput of NMQR 3152 has been slightly laterally compressed (Text-fig. 4). The supraoccipital and exoccipital bones are indistinguishably fused. Posterolaterally the occipital bones form a prominent ridge where they meet the squamosal. The tabular has a broadly triangular shape, with its apex extending downwards almost as far as the ventral limits of the squamosal to form a wedge-shaped contact with the squamosal on the lateral, and the occipital bones on the medial side. Dorsolaterally the tabular is in contact with the parietal, ventrolaterally with the squamosal, and dorsomedially with the postparietal. The tabular is relatively smaller than those of *Titanophoneus* and *Anteosaurus* in that it does not extend so far ventrally.

The postparietal is incompletely preserved on the dorsal, medial, and ventromedial sides. Only the most lateral portion of the supraoccipital is preserved and is in contact with the most ventral portion of the postparietal. A sinusoidal suture separates the postparietal and tabular. Almost two-thirds of the distance up the side of the postparietal, this suture curves laterally to meet the horizontal suture which forms the border between the tabular and parietal bones. The parietal thus borders on the postparietal on its dorsal and dorsolateral sides.

Lower jaw

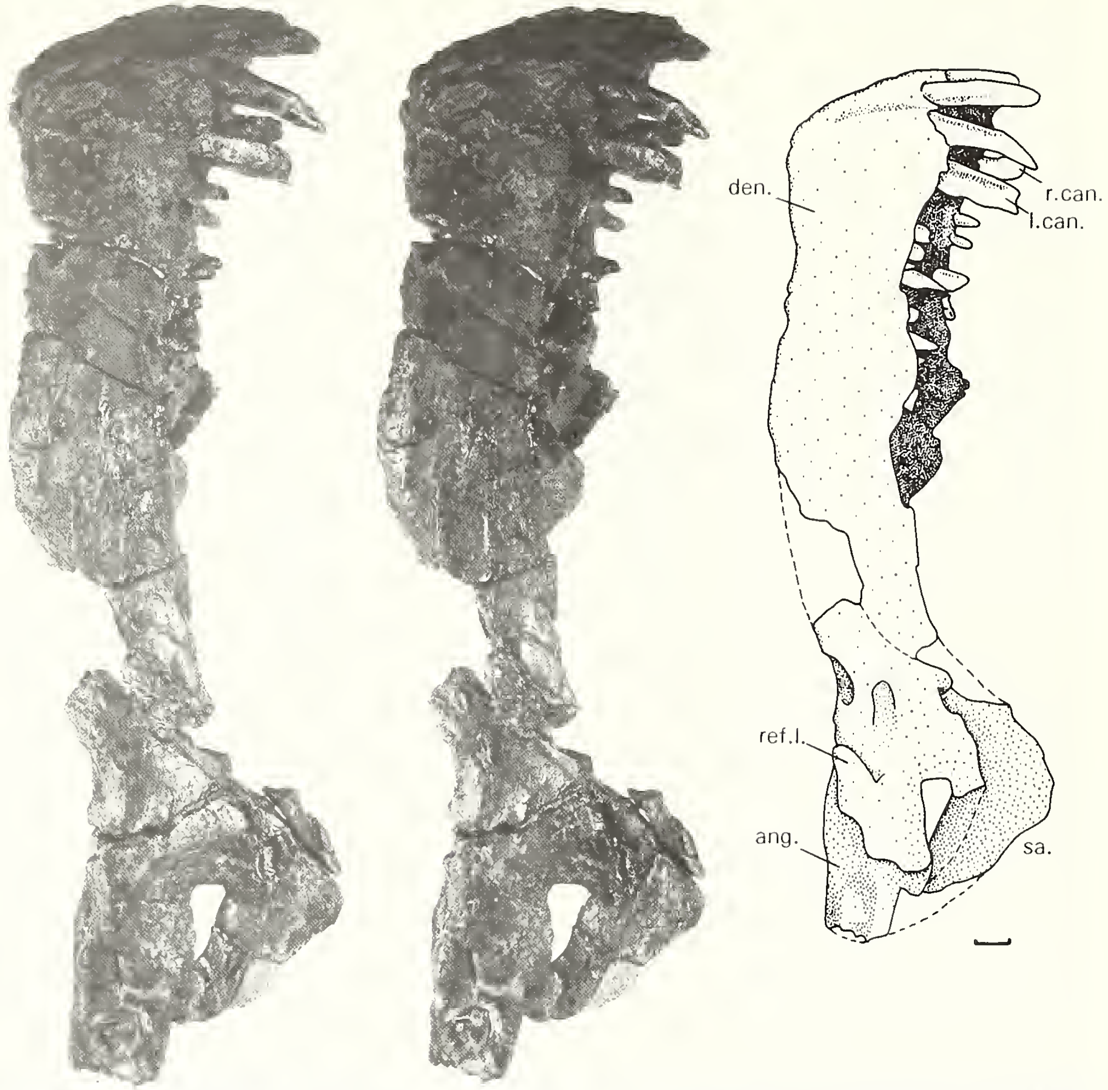
The lower jaw is relatively well preserved, with the left ramus being more complete than the right (Text-figs 5–7). Several of the teeth are in place. Portions of the ventral side of the jaw encompassing the contact area between the dentary and angular bones has been eroded away.

The dentary is the largest element of the lower jaw. Only the anterior portion of the left ramus is preserved, but the right ramus is almost complete with only the posteroventral portion weathered away. The anterior and anterolateral portion of the dentary (up to the level of the third postcanine) has a rugose surface texture which smooths out towards the posterior end. Immediately posterior to the lower canine, the lateral surface of the dentary forms a vertically orientated indentation to accommodate the upper canines which pass on the lateral side of the lower jaw when the jaws are occluded.

The dentary bears four incisors (Text-fig. 5), a single canine, and at least seven postcanines. As in *Syodon* and *Titanophoneus*, the three anteriormost incisors are relatively large. In *Australosyodon* only the root of the fourth incisor is preserved and it appears to have been smaller than the others. The tip of the first incisor is broken and badly weathered so that it is not possible to determine the morphology. Incisors 2 and 3 show signs of an incipient lingual heel. The left canine is better preserved than the right, is slightly ovoid in cross section and does not have a pronounced keel on the posterior side as is present in the upper canine. On the left ramus of the lower jaw, the postcanine dentition is complete and seven teeth are preserved, some more completely than others (Text-fig. 6). The right ramus has been distorted and the dentition is incomplete, so that it is difficult to be sure of the number of postcanines. It is estimated (counting the number of alveoli) that nine postcanines were present on this side of the jaw. When viewed from the side, all the postcanines except the last, slant slightly in a posterior direction, and have a pointed tip. The first three postcanines have a small incipient heel on the medial side, which does not appear to be present on the more posteriorly situated teeth. The last postcanine differs entirely from the rest in form. This tooth is elongated anteroposteriorly, and is flattened laterally. The crown of the tooth is not pointed but flattened. In *Syodon*, all the postcanine teeth on the lower jaw are more rounded in cross section, and have a sharp conical point. They also have slight keels (orientated anterolaterally and posteromedially) on their anterior and posterior sides. Because the jaws of the single specimen of *Titanophoneus* are tightly closed, it is not possible to determine the morphology of the crowns of the teeth.

The splenial is situated on the ventromedial side of the lower jaw, and, when viewed from the lateral side, protrudes slightly below the ventral edge of the dentary. Anteriorly the splenial is a narrow bone, which thickens posteriorly to reach its greatest thickness in the area below the fourth postcanine tooth. The posterior end of the splenial is not preserved and it is not possible to determine its relationship to the angular bone.

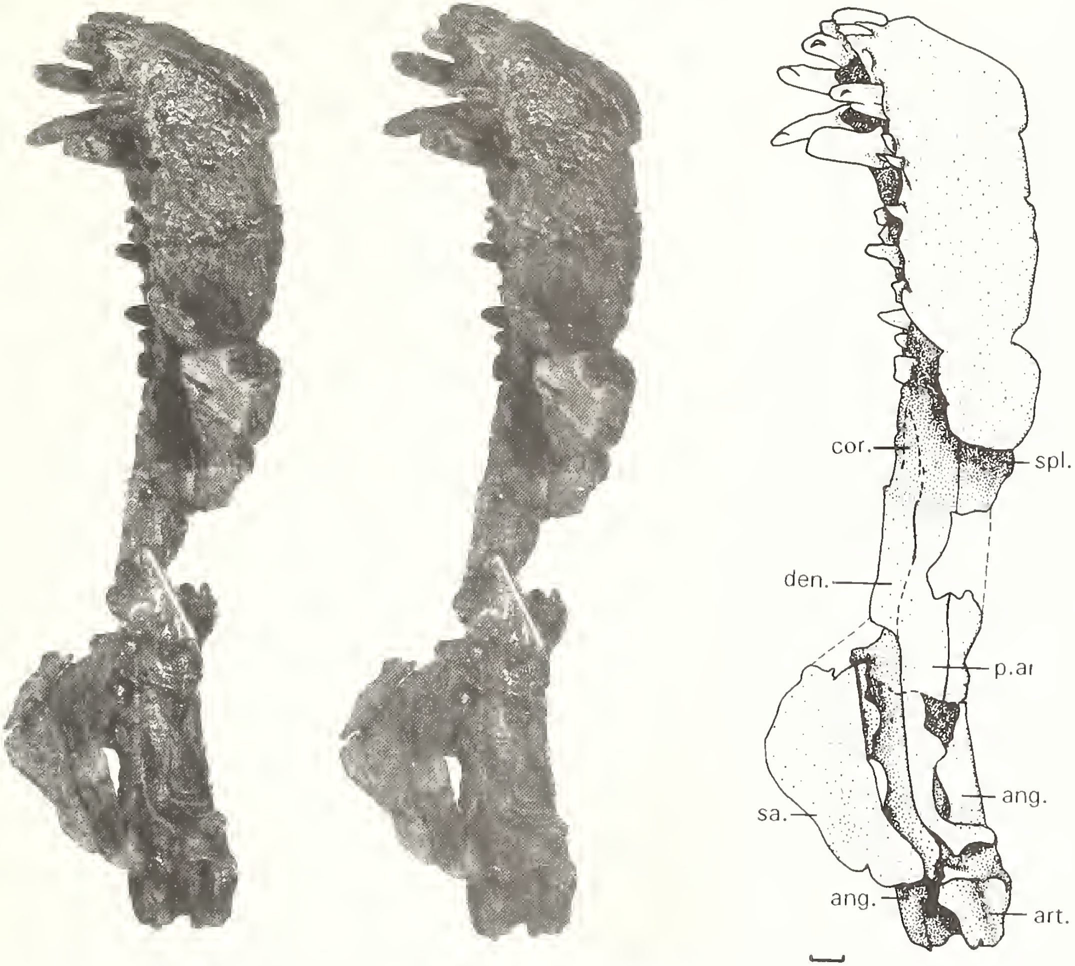
At the posterior end of the lower jaw, the angular forms the ventro-medial, ventral and most of the lateral side of the lower jaw. It tapers anteriorly to meet the dentary on the ventral side in a wedge-shaped contact



TEXT-FIG. 6. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of lateral view of lower jaw. Scale bar represents 10 mm.

when viewed from the lateral side. The angular has its greatest exposure on the lateral side and forms a prominent reflected lamina. The posterodorsal portion of the angular is not preserved, but a semicircular grooved imprint on the lateral side of the surangular suggests the dorsal limits of this bone which reaches its greatest height below the coronoid eminence. In *Syodon* and *Titanophoneus* the angular is extremely thin in this area and so is vulnerable to destruction. The angular is also visible on the ventromedial side of the lower jaw of *Australosyodon*. The anteromedial end of this bone is not preserved so that it is not possible to determine the relationship between the angular and coronoid.

The articular is a relatively large bone bounded by the angular laterally and ventrally, and the prearticular anteriorly. The dorsal surface of the articular has a W-shape to accommodate the articulatory condyles of the quadrate.

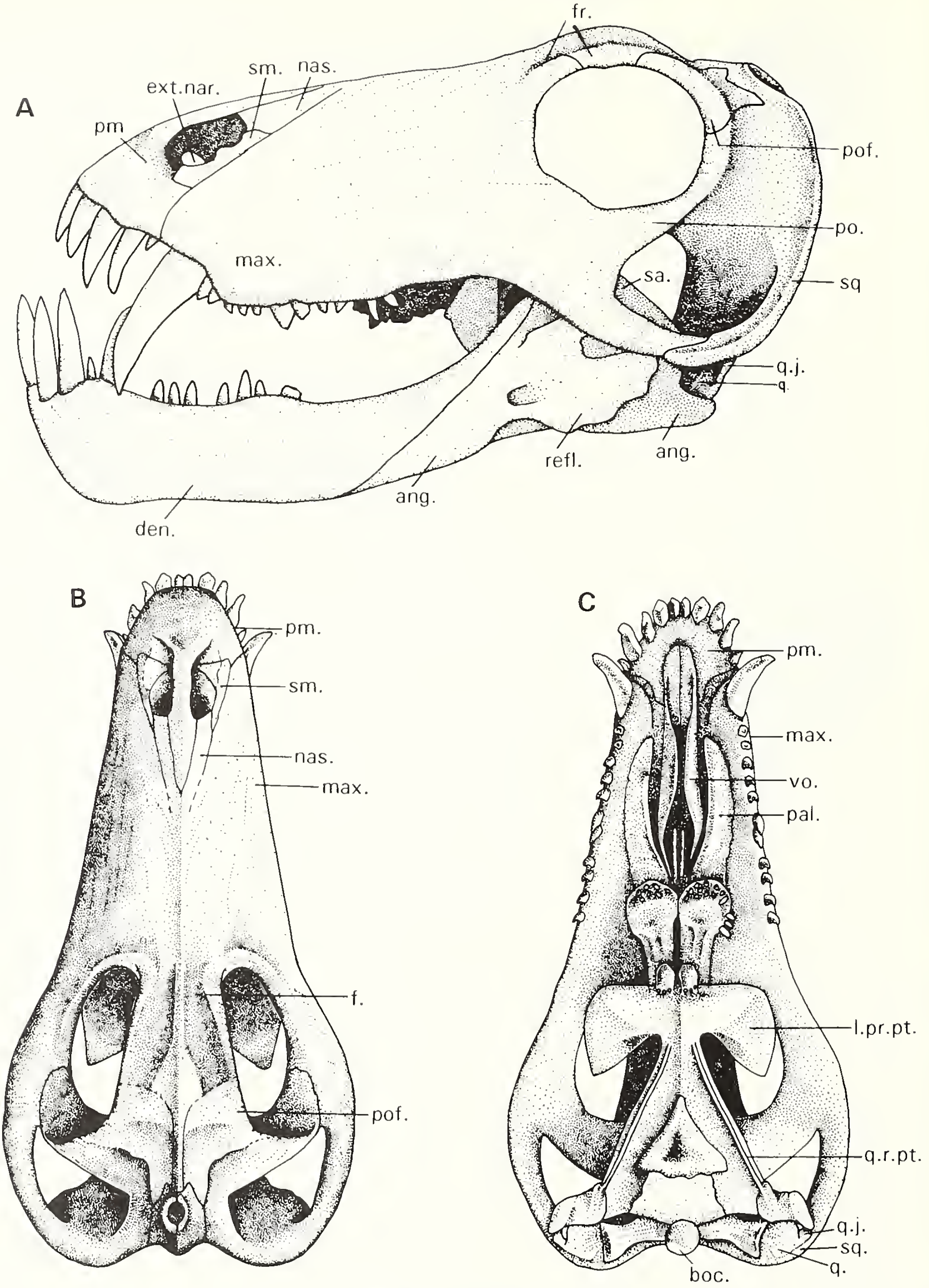


TEXT-FIG. 7. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of medial view of lower jaw. Scale bar represents 10 mm.

The prearticular is a long, narrow bone situated on the medial side of the jaw. At its posterior end it is in sutural contact with the articular, while it meets the angular on the ventral, medial and dorsal sides. Immediately in front of the articular bone, it curves in an anterodorsal direction before extending anteriorly on the medial side of the lower jaw. Anteriorly the prearticular lies against the dentary on the dorsal and lateral sides, and appears to meet the splenial on the ventral side. The nature of the contact with the splenial is not known as the anterior portion of the prearticular is not preserved.

Prior to fossilization, the surangular was displaced from the rest of the lower jaw and lay within the temporal opening of the skull. During preparation, this portion of the lower jaw was removed from the skull and fitted back on the lower jaw, with the result that its present position on the lower jaw (as figured), is the author's interpretation of the fit. This bone forms the posterodorsal extremity of the lower jaw and is visible from both the lateral and medial sides. It is bounded by the angular on the ventral and ventro-lateral sides, and the dentary on the anterior side.

The coronoid bone has been considered to be absent in dinocephalians, but such a bone has been noted in certain dinocephalian genera (Boonstra 1936, 1956; Hopson 1991; van den Heever and Grine 1991). It is difficult to determine with certainty whether a coronoid is present in NMQR 3152, but a small bony fragment, which tapers to a point at its anterior end, is situated on the dorso-medial surface of the dentary immediately



TEXT-FIG. 8. Reconstructions of the skull of *Australosyodon nyaphuli*, gen. et sp. nov. A, lateral view; B, dorsal view; C, ventral view; ×0·4.

behind the last postcanine and is strongly suggestive of a coronoid, both in its position and size. The concave area, which has a rugose surface, is present on the posterior portion of the dentary behind the tooth row in *Syodon* and may have been the area of attachment for the coronoid bone. No coronoid or its area of attachment could be determined in *Titanophoneus*.

DISCUSSION

King (1988) considered dinocephalians with a small heel on the incisor, a slight tendency toward pachyostosis, and the jaw articulation shifted slightly forwards, to belong to the Anteosauridae. *Anteosaurus*, the only anteosaurid dinocephalian so far described from South Africa, is considered the most derived genus of this family in that the postcanine dentition is more reduced, the postorbital region of the skull is deepened producing a deeper temporal fenestra, a boss is present on the external surface of the angular (King 1988). As NMQR 3152 is clearly an anteosaurid dinocephalian but lacks the apomorphic characters of *Anteosaurus*, it is considered to be more closely allied to the primitive anteosaurid dinocephalians previously known only from Russia.

Several genera of primitive anteosaurid dinocephalians (brithopodine dinocephalians of King 1988) have been described, but many of them are based on individual postcranial elements. As the new material consists only of a skull, the genera based on postcrania alone cannot be considered for the purposes of comparison. Of the described genera, the only ones which have reasonable cranial material preserved, and can be compared with *Australosyodon* are *Archaeosyodon*, *Doliosauriscus*, *Notosyodon*, *Syodon* and *Titanophoneus*.

Archaeosyodon is represented by several incomplete skulls and fragments from the Ocher Complex. It is much larger than NMQR 3152, has teeth on the lateral flange of the pterygoid, as well as numerous teeth on the palatine and pterygoid bosses, and in these aspects alone is so different from the specimen under discussion that it need not be considered for further comparison.

Notosyodon is represented by the posterior portion of a skull, some isolated teeth, and a fragment of the left dentary, all from separate individuals. Because the posterior region of the anteosaurid skull does not have many diagnostic features, it is difficult to compare the holotype of *Notosyodon* with that of *Australosyodon*. There are, however, some obvious differences in that the dorsal edges of the orbits are more thickened (pachyostosed) than in *Australosyodon*, and the interorbital portion of the skull roof lacks the median ridge present in both *Australosyodon* and *Syodon*.

Doliosauriscus, *Syodon* and *Titanophoneus* have been well described in the literature (Orlov 1958). The degree of pachyostosis of the skull roof varies among these primitive anteosaurid genera. In *Doliosauriscus* the bone thickening is very pronounced, particularly the bones above the orbit and of the skull vault, and is very different from the new specimen. In *Titanophoneus* the thickening is restricted to the prefrontal and the dorsal border of the orbit, and in *Syodon* there is very little thickening and this is only on the dorsal border of the orbit (Orlov 1958). *Australosyodon* is similar to that of *Syodon* in that the skull roof is only slightly thickened on the dorsal border of the orbit.

As in *Syodon* and *Notosyodon*, the anterior wall of the pineal boss in *Australosyodon* is formed by the frontal and parietal bones, and not just the parietal as in *Doliosauriscus* and *Titanophoneus* (Orlov 1958). In both *Syodon* and *Australosyodon* the pineal boss forms the medial border of the area of attachment of the jaw adductor musculature, while in *Doliosauriscus* and *Titanophoneus* a ridge is present on the lateral side of the pineal boss and prevents muscle attachment on the boss. The frontal forms the anterior border of this depressed area of origin of jaw adductor musculature in *Australosyodon* and *Syodon*, but in *Doliosauriscus*, *Notosyodon* and *Titanophoneus* the frontal does not extend sufficiently far posteriorly to border on this depression. The situation in *Notosyodon*, as regards this feature, is transitional between that of *Titanophoneus* and *Syodon*.

The vomer is not completely preserved in *Doliosauriscus*, *Notosyodon* or *Titanophoneus* but in both *Australosyodon* and *Syodon*, where it is preserved, the lateral sides curve ventrally and toward the medial suture. The ventrally protruding tuberosities of the palatine of the new specimen are relatively large and prominent, and in this respect more closely resemble those of *Syodon*, rather than *Titanophoneus* or *Doliosauriscus* where the palatine bosses are smaller and less prominent

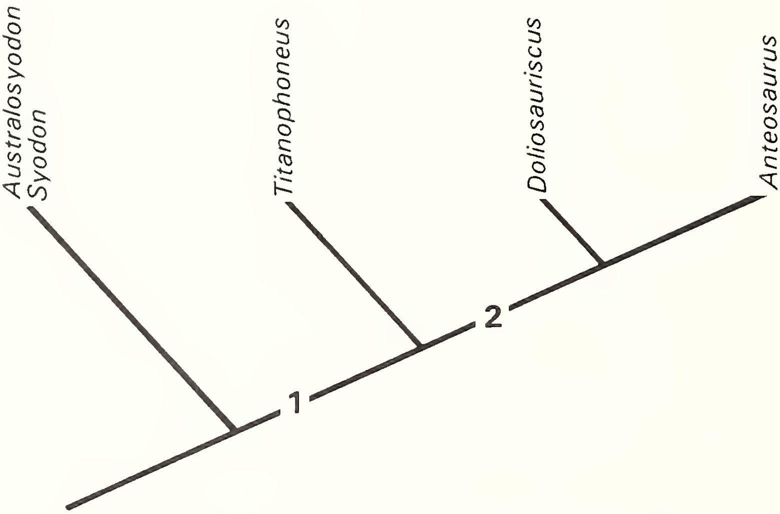
(Orlov 1958). *Australosyodon* has twelve to fourteen teeth on the palatine boss which is many more than the seven to eight of *Titanophoneus*, and is similar to the nine to thirteen of *Syodon*, and the ten to thirteen of *Doliosauriscus* (Orlov 1958).

The same trend is reflected in the ratio of the transverse diameter of the palatine bosses to that of the lateral flange of the pterygoid. This ratio is 1:3 for *Titanophoneus*, 2:3 for *Syodon* (Orlov 1958), and 2:3 for *Australosyodon*. No teeth are present on the lateral flanges of the pterygoid in *Australosyodon*. This differs from the situation in *Titanophoneus* (two large), *Syodon* (four small), and *Doliosauriscus* (three small) (Orlov 1958). The median tuberosity of the pterygoid of *Titanophoneus* and *Doliosauriscus* is small and does not bear teeth (Orlov 1958), whereas in both *Australosyodon* and *Syodon* it is large and teeth are present. The boss of *Australosyodon* is, however, much larger than that of *Syodon*.

The canine teeth of the new specimen are slightly laterally compressed and have a slight keel on the posterior side. In this respect it more closely resembles the situation in *Titanophoneus* where the canine is flattened, rather than in *Syodon* or *Doliosauriscus* where the canine is more rounded (Orlov 1958).

The shape of the postcanine teeth of *Titanophoneus* is uniform for all the teeth (Orlov 1958), whereas in the lower jaw of *Syodon* and the new specimen the crowns of the anteriormost teeth have sharp points, and the posterior two teeth have a blunt point and are wider, possibly for crushing. The length of the tooth rows of the upper and lower jaws of *Doliosauriscus* and *Titanophoneus* are the same whereas in *Syodon* and *Australosyodon* the tooth row of the upper jaw is longer than that of the lower such that the posterior postcanines of the upper jaw are unopposed (Orlov 1958).

In the lower jaw, both *Doliosauriscus* and *Titanophoneus* have a boss on the lateral surface of the angular (Hopson and Barghusen 1986). This feature is not present in either *Syodon* or *Australosyodon*, and thus seems to be coupled with the more pachyostosed skulls of *Doliosauriscus* and *Titanophoneus*.



TEXT-FIG. 9. Cladogram illustrating the relationships of anteosaurid dinocephalians (modified after Hopson and Barghusen 1986). Apomorphies for each node are: 1, lateral surface of angular has thickened area ('boss') adjacent to dentary. 2, prominent 'boss' on angular; dorsal surface of nasal, frontal and postfrontal bones pachyostosed.

CONCLUSION

It is evident that *Australosyodon* is very primitive anteosaurid dinocephalian and, as such, is the first from the southern hemisphere.

In its cranial features, *Australosyodon* most closely resembles *Syodon*, but differs in several respects: the palatine bosses of the new specimen do not protrude as far ventrally as those of *Syodon*; the anterior edge of the boss slopes gently in an antero-dorsal direction; no teeth are present on the lateral flange of the pterygoid, but at least seven teeth are present on the pterygoid boss which is larger than in *Syodon*; the canine is not rounded in cross section as in *Syodon*, but is ovoid with a slight keel which is more prominent on the posterior edge of the tooth; teeth on the maxilla and dentary less robust than those of *Syodon*; as in *Syodon* a longitudinal medial ridge extends down the midline of the frontal, but differs from that in *Syodon* in that it expands laterally to form a prominent medially situated boss above the orbits, before continuing posteriorly as a ridge right up to the pineal boss; contact of the frontal bone on the dorsal border of the orbit is slightly greater than in *Syodon*.

Syodon is considered to be the least derived genus of anteosaurid dinocephalian because it lacks a thickened area ('boss') on the angular adjacent to the dentary (Hopson and Barghusen 1986). As this feature is also absent in *Australosyodon* and in other aspects of its cranial morphology the new genus is most similar to *Syodon*, it would appear that *Australosyodon* is also one of the most primitive anteosaurid dinocephalians (Text-fig. 9). This specimen, the first skull of a primitive anteosaurid reported from outside Russia, is thus of great palaeobiogeographical consequence and, together with the rest of the primitive therapsid fauna from the same biozone, strongly suggests that the most primitive therapsids are present in South Africa as well as Russia.

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ABBREVIATIONS

ang.	angular	lac.	lachrymal	pt.	pterygoid
art.	articular	l.pr.pt.	lateral process of pterygoid	q.	quadrate
can.	canine	max.	maxilla	q.j.	quadratojugal
cm	centimeter	nas.	nasal	q.r.pt.	quadrate ramus of pterygoid
cor.	coronoid	op.	opisthotic	r.can.	right canine
den.	dentary	pal.	palatine	ref.l.	reflected lamina
e.a.m.	external auditory meatus	p.art.	prearticular	sa.	suragular
ext. nar.	external naris	par.	parietal	sm.	septomaxilla
fr.	frontal	p.for.	pineal foramen	spl.	splenial
i.	incisor	pmx.	premaxilla	sq.	squamosal
j.	jugal	po.	postorbital	t.	tabular
l.can.	left canine	pof.	postfrontal	v.	vomer

PHYLOGENY AND PALAEOBIOLOGY OF *MARSUPITES* AND *UINTACRINUS*

by CLARE V. MILSOM, MICHAEL J. SIMMS *and* ANDREW S. GALE

ABSTRACT. The Upper Cretaceous *Marsupites* and *Uintacrinus* are among the morphologically most unusual of all fossil crinoids. Both have a large theca, ten extremely long arms, and lack any anchoring structure in both adult and juvenile stages; this morphology appears so unlike that of other articulate crinoid groups that earlier attempts to identify possible sister groups have been inconclusive. Cladistic analysis indicates that both genera are closely related to the Comasteridae, with *Uintacrinus* being less derived than *Marsupites*. Both genera have a virtually world-wide distribution through a limited stratigraphical interval within the Santonian Stage. Their widespread distribution, combined with the absence of a mode of attachment, has led to the conclusion that they were pelagic. However re-examination of their morphology indicates that *Marsupites* and *Uintacrinus* were benthic. The global distribution of these taxa probably reflects a long-lived planktotrophic larval stage in the life cycle.

IN 1821, J. S. Miller published his 'Natural History of the Crinoids, or Lily-shaped Animals' in which he outlined a scheme which still forms the basis of their classification. Among the many fossil crinoids which he described was a bizarre form from the Chalk of southern England. It possessed a large cup composed of three circlets of plates and a single centrodorsal plate at the base. There was no trace of a stem or cirri arising from the centrodorsal as in the other stemless group of which Miller was aware, the comatulids. He named it *Marsupites ornatus* on account of its similarity to a purse, or marsupium, and the ornamented nature of the plates. It had earlier been described by Parkinson (1808), as the 'Tortoise Encrinite', and by Schlotheim (1820) as *Fungites testudinarius*, although Miller was the first to appreciate its stemless nature.

Marsupites was originally a manuscript name used by Gideon Mantell and published in the following year (Mantell 1822). In 1876, a large crinoid from the Niobrara Chalk of Kansas was described under the name *Uintacrinus socialis* by Grinnel, who noted its similarity to the English *Marsupites*. Two years later, the stemless nature of *Uintacrinus* was confirmed by additional material from the Upper Chalk of Westphalia, described as a distinct species *Uintacrinus westfalicus* (Schlueter, 1878). Subsequent discovery of several large groups of *Uintacrinus socialis*, the largest covering ninety five square metres and including more than 1200 individuals, led to a series of publications culminating in Springer's monumental work on the structure and relations of *Uintacrinus* (Clark 1893; Williston and Hill 1894; Bather 1896; Springer 1899, 1900). However, despite these exhaustive descriptions and a number of subsequent publications (Clark 1911; Sieverts 1927; Rasmussen 1961), a great deal of uncertainty has continued to surround their phylogenetic position and possible mode of life. The purpose of the present contribution is to assess the phylogeny and palaeobiology of *Marsupites* and *Uintacrinus*.

Terminology of the crinoid endoskeleton used herein follows Ubaghs (1978).

GENERAL MORPHOLOGY

Exhaustive accounts of the morphology of *Marsupites* were given by Sieverts (1927) and Rasmussen (1961, 1978). The morphology of *Uintacrinus* has been described by Bather (1896), Springer (1901) and Rasmussen (1961, 1978).

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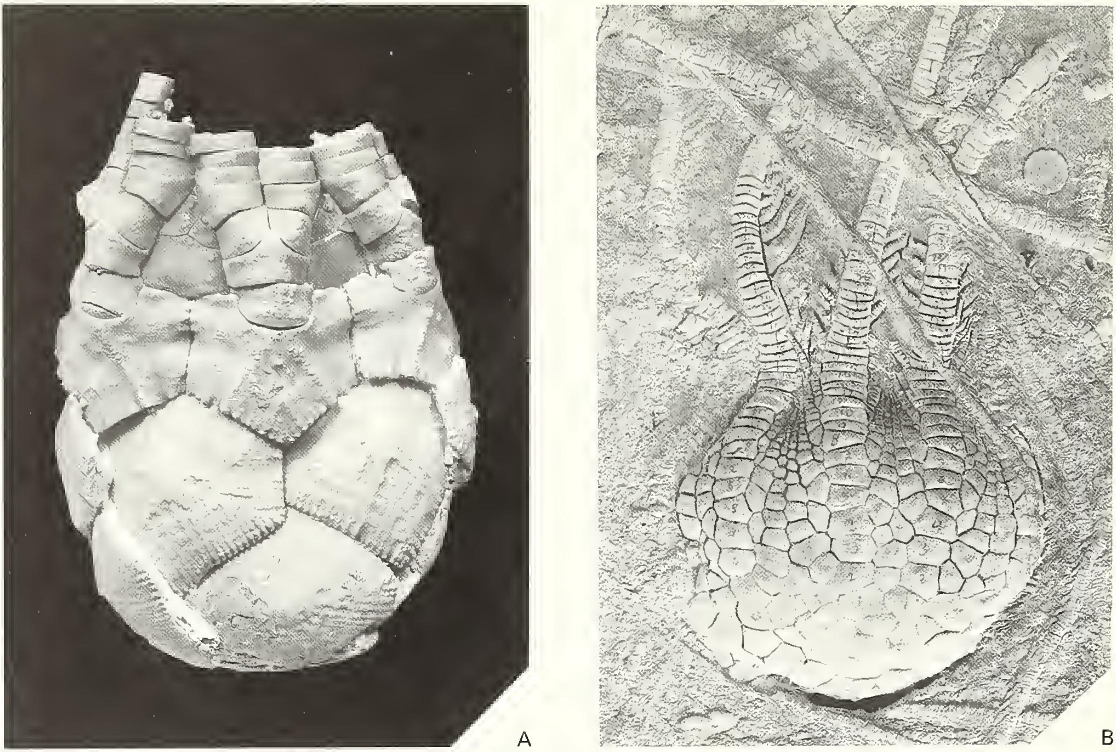
In *Marsupites*, the calyx is large. Mature specimens are commonly 65 mm high and 60 mm in diameter. It is sub-globose to oval in shape and composed of sixteen polygonal plates which are united by straight sutures (Text-fig. 1A). In general, the plates from stratigraphically older specimens are smooth, whilst in younger specimens they become more ornate and are sculpted with a series of narrow straight ridges or rows of granules. Structurally, the plates are formed of two calcitic layers. An outer regular network of calcite covers a less dense internal layer. Thecal plates are arranged in three circlets around a dorsal centrale. The plate circlets have been interpreted as radials, basals and infrabasals. A tegmen is unknown.



TEXT-FIG. 1. Calyces of *Marsupites* and *Uintacrinus*; from the collections of the Natural History Museum, London. A, *Marsupites testudinarius*; E14261; *M. testudinarius* Zone, Upper Chalk; Brighton, Sussex, England; calyx with interbrachial plates; × 1·4. B, *Uintacrinus socialis*; E6328; Smokey Hill Formation, Santonian; Elkader, Kansas, USA; calyx and arms; × 0·85.

The length of arms is unknown for *Marsupites*. They are sharply demarcated from the theca, and are believed to bifurcate only once on the second primibrach. Small, thin, interbrachial plates which cover the area between the radials and the brachials are present up to approximately $IIBr_3$. The articulations at IBr_{1-2}, $IIBr_{1-2}$ and $IIBr_{3-4}$ were described by Rasmussen (1961) as syzygial. However, due to the paucity of culmina on the facets, he commented that they resemble a synarthrial articulation. These articulations were described more accurately by Clarke (1909) as pseudosyzygies. Muscular articulations, which are consistently straight, occur at $RR\text{–}IBr_1$, $IBr_2\text{–}IIBr_1$, $IIBr_{2-3}$ and $IIBr_{4-5}$. Distally, they become more common. Syzygial articulations in which the culmina are finer and more numerous are generally found within the intervals $IIBr_{4-8}$ and $IIBr_{8-13}$. Pinnule sockets are found from $IIBr_2$ onwards in the distal ends of the brachials with muscular articulations.

Uintacrinus has a large, globose theca. Mature specimens are normally 62·5–75·0 mm in diameter. The theca is composed of a variable number of smooth, slightly arched, polygonal plates. There are five radials, five basals, occasionally five infrabasals and a centrale (Text-fig. 1B). In addition, there are three types of supplementary plates (Bather 1896): interbrachials, interdistichials and interpinnulars. These are positioned above the radials between the fixed brachials. The ventral surface is covered by a tegmen which is preserved as a carbonized membrane studded with small irregular calcareous grains.

The length of arm branches in *Uintacrinus* is extremely difficult to measure. Despite the frequency with which articulated arm sections are preserved, arms are invariably tangled and interlaced. Based on the rate of arm tapering in a single arm, Bather (1896) concluded that the minimum arm length was 0·9 m. Using a similar technique, Springer (1901) concluded that the arm length was 1·25 m. The arms branch only once, at IBr_2. They are not clearly demarcated from the theca, with a varying number of brachials, up to IIBr_8, being fixed in the thecal structure. Muscular articulations are found at RR–Br_1, IBr_2–IIBr_1, IIBr_{2-3} and further distally. IBr_{1-2} are syzygial. Syzygies also occur further distally at frequent intervals interspersed with muscular articulations. The first fixed pinnule is given off from IIBr_2 on the outer side of the ray. Thereafter, pinnules are connected to IIBr_4, IIBr_5, IIBr_7, IIBr_9 on alternate sides of the brachial. From IIBr_{10}, pinnules occur on every brachial, except where the distal articulation is syzygial. All pinnular sockets are muscular.

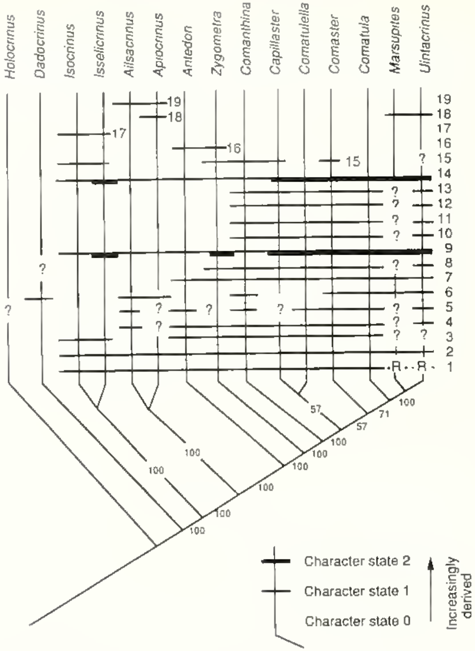
PHYLOGENETIC ANALYSIS OF *MARSUPITES* AND *UINTACRINUS*

The cladistic approach stresses the similarities between taxa as a means of identifying homologies. This is an essential step in any attempt to reconstruct the phylogeny of a particular group upon which a more natural classification can then be based. Crinoids, with their complex, multi-element skeletons, are ideal subjects for this approach. *Marsupites* and *Uintacrinus* inherently lack any of the suite of characters present in the column of most other crinoids, but the available characters nonetheless enable comparisons to be made with various groups with which affinities have been suggested in the past.

The cladogram in Text-figure 2 incorporates representatives of all articulate crinoids which have been considered as possible sister taxa to *Uintacrinus* and *Marsupites*. Palaeozoic taxa have been excluded since it has been shown by Simms and Sevastopulo (1993) that the articulates are a monophyletic taxon derived from a single Late Palaeozoic group of cladids. No close relationship exists between any disparid or camerate taxon and any post-Palaeozoic crinoid. The data were analysed using the PAUP program on an Apple Macintosh IIsi. Five hundred bootstrap replications were undertaken, with the relatively small number of taxa (fifteen) and characters (nineteen) allowing a branch-and-bound search. *Holocrinus*, the oldest and the most stemward articulate crinoid known, was selected as outgroup and the characters were initially unweighted. The data matrix is reproduced along with the cladogram in Text-figure 2.

A total of twenty-eight possible trees were obtained from the original data. The Consistency Index (CI) was 0·600; the Retention Index (RI) was 0·788. Throughout, *Uintacrinus* and *Marsupites* were grouped together as sister taxa and maintained a constant position as derived sister group to the comasterids. The one area of inconsistency lay among the five comasterid taxa. In a strict consensus of twenty-eight trees, the relationship of these five taxa was entirely unresolved. However, characters were reweighted by the maximum value of the rescaled consistency index, and a further branch-and-bound search undertaken. This was undertaken three times consecutively to enhance resolution. Seven trees were obtained. *Comanthina* was consistently placed as the least derived taxon but the relationship of the four remaining taxa was resolved only at the fifty per cent Majority-rule consensus of the seven trees. This is the cladogram reproduced in Text-figure 2.

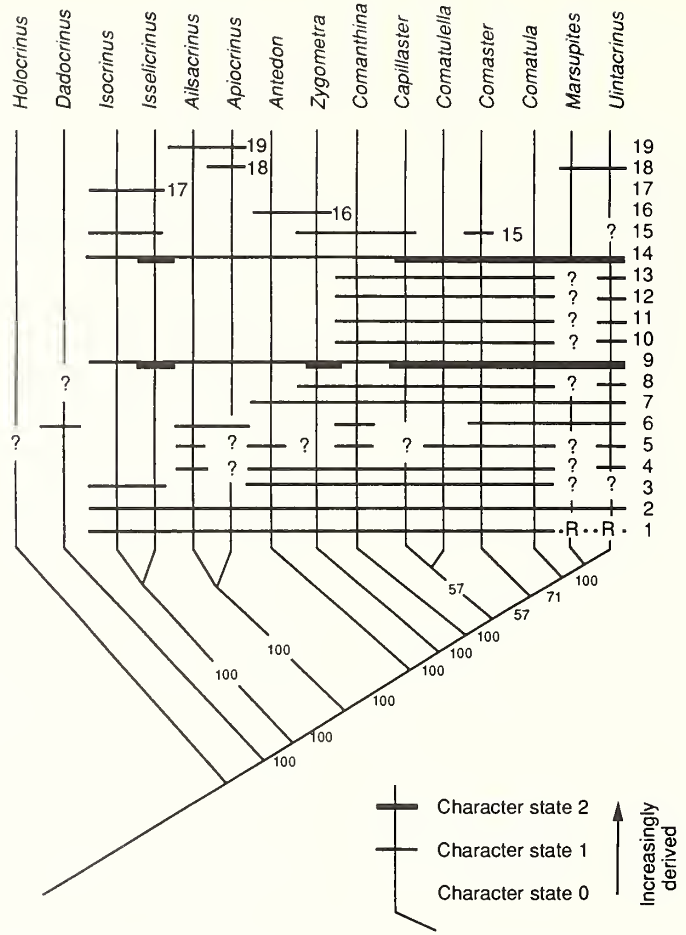
This analysis confirms the close phylogenetic relationship of *Marsupites* and *Uintacrinus* with the extant Family Comasteridae, a conclusion first reached in part by Springer (1901). However, a rather surprising result of the analysis is the consistent position of the millericrinids, *Apiocrinus* and *Ailsacrinus*, rather than the isocrinids, *Isocrinus* and *Isselicrinus*, as a sister group to the comatulids.



TEXT-FIG. 2. Data matrix and fifty per cent Majority-rule consensus of seven trees for *Marsupites*, *Uintacrinus* and other selected articulate crinoids. Figures shown give percentage support for each node in the cladogram. Characters are listed below. R = character reversal

1, Infrabasals exposed (0) / cryptic (1). 2, Axial canal in brachials paired (0) / single (1). 3, Larval stem articula synostosial (0) / synarthrial (1). 4, Tegmen tessellate (0) / of scattered plates (1). 5, Grooveless arms or pinnules absent (0) / present (1). 6, Cirri present in adult (0) / absent (1). 7, Stem present in adult (0) / absent (1). 8, Ambulacral grooves with cover plates (0) / without (1). 9, IBr_{1-2} syzygial (0) / synarthrial (1) / pseudosyzygial (2). 10, Mouth central (0) / marginal (1). 11, Anal cone central (0) / marginal (1). 12, Ambulacra endocyclic (0) / exocyclic (1). 13, Proximal pinnules straight (0) / with combs (1). 14, $IIBr_{1-2}$ syzygial (0) / synarthrial (1) / pseudosyzygial (2). 15, Arms divide once (0) / more than once (1). 16, Basals discrete (0) / fused to rosette (1). 17, Stem without cryptosymplexies (0) / with them (1). 18, Interbrachial plates absent (0) / present (1). 19, Syzygy at $IIBr_{3-4}$ (0) / at $IIBr_{4-5}$ (1).

This may be, in part, a consequence of the small size of the database analysed, but it also stresses the need to investigate the phylogenetic position of the millericrinids, a rather poorly understood group, in greater depth



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PREVIOUS IDEAS ON THE PHYLOGENETIC POSITION OF *MARSUPITES* AND *UINTACRINUS*

There has been no clear consensus on the origin and affinities of *Marsupites* and *Uintacrinus*. This is reflected in their current taxonomic status, in which the two genera are assigned to separate families within a distinct order, the Uintacrinida, comprising only three species in total. This has arisen through a tendency to stress the differences between taxa rather than the similarities (Paul and Smith 1988). It is comparable with the situation amongst many early Palaeozoic echinoderms, in which numerous small, short-lived groups were elevated to the rank of Class (Sprinkle 1973). Many taxa have, at some time or other, been associated with *Uintacrinus* and *Marsupites*. These are discussed below.

Palaeozoic crinoids

Marsupites and *Uintacrinus* have been assigned to various Palaeozoic crinoid taxa, including cladids, flexibles and camerates. *Uintacrinus* bears a superficial similarity to some flexible crinoids (e.g. *Forbesiocrinus*) in the development of interbrachial plates. The theca of *Marsupites*, with its large infrabasals and ornate thecal plates, is reminiscent of many camerates and some cladids, such as *Rhodocrinites* and *Sphaerocrinus*. However, both *Marsupites* and *Uintacrinus* share numerous synapomorphies with the exclusively post-Palaeozoic subclass Articulata, notably the pinnulate arms branching at IBr_2, muscular articulations on most brachials, a single axial canal piercing each brachial, ligamentary articulations at IBr_{1-2}, IIBr_{1-2}, IIBr_{3-4} and at intervals beyond, and the absence of an anal plate in the dicyclic or cryptodicyclic cup. These characters are largely absent from any suggested Palaeozoic ancestors (Simms and Sevastopulo 1993).

Dadocrinus

Bather (1896) first suggested that the Middle Triassic genus *Dadocrinus* represented the closest known relative to *Uintacrinus*, a hypothesis supported by Kirk (1911). At that time, *Dadocrinus* was considered intermediate between the Articulata and the Palaeozoic Erisocrinidae. *Dadocrinus* is now recognized as a uniserial member of the exclusively Triassic family Encrinidae, other representatives of which bear a superficial similarity to the Palaeozoic Erisocrinidae. Among the characters of *Dadocrinus* which Bather (1896) considered as evidence for a link with *Uintacrinus* are the cryptodicyclic cup, the pinnulate arms branching only once on the second primibrach, and the axial canal in the thecal and brachial plates. However, these are characteristic of most, if not all, articulates. The primibrachs of *Dadocrinus* and *Uintacrinus* are also united by interbrachials but this is not unique to these taxa. A similar arrangement is also found in the Pentacrinitidae, Apiocrinitidae and many Palaeozoic taxa, suggesting widespread homoplasy in this character. Bather (1896) also considered the arrangement of syzygies in the arms of *Dadocrinus* to indicate a close relationship with *Uintacrinus*, but this too is a plesiomorphic character shared also by the Palaeozoic stem group of the articulates (Simms and Sevastopulo 1993). However, although the non-muscular articulations in the arms of most early Triassic taxa were syzygial throughout, in most later taxa the more proximal articula, those at IBr_{1-2} and IIBr_{1-2}, were modified into synarthrial articula. *Marsupites* and *Uintacrinus* are comparatively unusual in that they represent post-Triassic taxa in which these particular articulations would appear to have retained the primitive, syzygial, condition. However, these syzygial articula have fewer and coarser crenulae than those further distally in the arms, and were described by Rasmussen (1961) as 'somewhat resembling a synarthrial articulation'. It would appear that rather than representing true syzygies, they in fact represent a modification of synarthrial articula, as demonstrated by Clarke (1909). The apparent similarities of articulation style in the arms of *Dadocrinus* and *Uintacrinus* are due, in part, to convergence.

Millericrinida

A close phylogenetic relationship between *Marsupites*, *Uintacrinus* and the millericrinid Apiocrinitidae was suggested by Pisera and Dzik (1979), based largely on the development of the interbrachial plates in the two groups, a character already suggested as prone to homoplasy. They admitted that there was otherwise a considerable morphological distance between them. Furthermore, *Apiocrinus* has the characteristic millericrinid synapomorphy of a syzygial articulation at $IIBr_{4-5}$ rather than at $IIBr_{3-4}$ as in *Marsupites*, *Uintacrinus* and most other articulates (Taylor 1983). Also, the stem is thick and well developed in *Apiocrinus* itself, although a related millericrinid genus, *Ailsacrinus* (Taylor 1983), has a greatly reduced stem.

Comatulida

Marsupites and *Uintacrinus* have been grouped with the comatulids on a number of occasions, although sharing few obvious homologies with them. Typical comatulid taxa, such as *Antedon*, resemble *Marsupites* and *Uintacrinus* only in the absence of a stem in the adult and in the weak plating of the tegmen. Otherwise their morphology is essentially plesiomorphic, retaining characters of their sister group the Pentacrinitidae.

Marsupites and *Uintacrinus* have articula at IBr_{1-2} and $IIBr_{1-2}$ which resemble syzygies, though they appear to represent secondarily modified synarthrial articula. Clark (1909) coined the term 'pseudosyzygy' for this type of articulation, although Moore and Teichert (1978) incorrectly regarded pseudosyzygy as a synonym of cryptosyzygy, the latter term generally being applied to poorly defined syzygial articula found in many isocrinids. Pseudosyzygies are found at IBr_{1-2} and $IIBr_{1-2}$ in several genera of the comasterids and in the isselicrinids (Simms 1988). In *Comaster*, the pseudosyzygial articula found in the adults develop from cryptosynarthries in the juveniles. *Marsupites* and *Uintacrinus* are united with the Comasteridae by a suite of distinctive synapomorphies. These synapomorphies led Springer (1901) to consider a close relationship between *Uintacrinus* and the Comasteridae, although he still maintained that *Marsupites* was sufficiently distinct as to be referred to the subclass Inadunata. Among the characters which Springer felt united *Uintacrinus* and *Comatula* (= *Actinometra* of his account) was the structure of the oral surface. In the great majority of articulates where it is known, the mouth is central and the anal tube marginal. Among comasterids, this condition is encountered only in some small or juvenile individuals; the remainder have a central anal tube and a marginal or subcentral mouth. The preservation of many of the specimens of *Uintacrinus* is sufficient to reveal that the configuration of the oral surface in this genus is identical to that in comasterids. Because of this arrangement of mouth and anus, the ambulacral grooves on the tegmen of both *Uintacrinus* and the Comasteridae are modified into a horseshoe-shaped, or exocyclic, configuration around the anal tube. Further similarities are also seen in the ambulacral system. In both taxa, cover-plates and side-plates are entirely absent from both arms and pinnules.

These characters (the development of pseudosyzygies and the unique structure of the tegmen and ambulacral system) suggest a close phylogenetic relationship between *Uintacrinus* and the Comasteridae, in particular with the extant genera *Comaster* and *Comatula*. Other similarities also exist which, although less distinctive than those just discussed, lend further support to suggestions of a sister group relationship. The centrodorsal in all three comasterid genera cited is small and low, with only a few small cirri at most. In adult specimens, it is often reduced still further, to a small pentagonal or stellate plate lying flush with the radial circlet and lacking cirral sockets altogether; this invites comparison with the centrale of *Uintacrinus*.

The Zygometridae appear to be a plesiomorphic sister taxon to the Comasteridae and Marsupitidae (*Marsupites* and *Uintacrinus*). They retain cirri on the centrodorsal, have a central anus and marginal mouth, and arms which divide several times. They also have spines on the distal ossicles of the cirri, a synapomorphy which they share with the Comasteridae, while the ambulacral skeleton is poorly developed by comparison with many comatulids. Furthermore, although the articulation at IIBr_{1-2} retains the plesiomorphic synarthrial arrangement, that at IBr_{1-2} is the more derived pseudosyzygial type characteristic of comasterids and maruspitids.

These comparisons indicate that *Uintacrinus* has a close phylogenetic relationship with the extant comatulid family Comasteridae. However, much of the data on which this is based is due to the fortuitous preservation of the arms and oral surface in many specimens of *Uintacrinus*. Similar data for *Marsupites* are lacking; although many intact thecae are known, some with the proximal parts of the arms preserved, details of the ambulacral system and the oral surface remain unknown. Thus, the evidence for *Marsupites* having close phylogenetic links with the Comasteridae is less convincing than for *Uintacrinus*, although comparison of *Marsupites* with *Uintacrinus* suggests that they are sister taxa.

SIMILARITIES BETWEEN *MARSUPITES* AND *UINTACRINUS*

Despite their overall morphological similarity and almost coincident stratigraphical distribution, *Marsupites* and *Uintacrinus* have frequently been considered as only distantly related, and have even been grouped in different subclasses. This has arisen largely through the tendency of earlier workers to compare differences between the two genera rather than similarities. The most striking difference, albeit superficial, lies in the construction of the cup. In *Marsupites*, the thecal plates are large, approximately equal in size and arranged in three circlets. These have been interpreted as the radials, basals and infrabasals, with a centrale at the base, and typically ornamented with radiating ridges. In contrast, *Uintacrinus* has much smaller thecal plates which are a little larger than the brachials. Both two-circlet and three-circlet forms of *Uintacrinus* are known; both forms have a small centrale at the base of the cup.

The arms in *Marsupites* and *Uintacrinus* are very similar, at least as far as can be judged from the limited data available for the former. Both have arms which divide only once on IBr_2 and have pseudosyzygial articulations at IBr_{1-2} and IIBr_{1-2}. Interbrachial plates are a distinctive feature of *Uintacrinus* and are almost as well developed, although rarely preserved, in *Marsupites*. The overall shape of the brachials differs very little between the two genera, with configuration of the distal articulum being strikingly similar. In both taxa, this latter articulum, which is straight muscular, is considerably narrower than the total width of the radial itself and is deeply excavated. The final and perhaps most obvious synapomorphy of these two genera is the absence of a stem at all known growth stages.

EVOLUTION OF *MARSUPITES* AND *UINTACRINUS*

The sudden, apparently inexplicable, appearance of *Marsupites* and *Uintacrinus* in the Late Cretaceous has remained one of the enigmas of post-Palaeozoic crinoid evolution. Their morphology appears so unlike other articulate crinoids that attempts to identify possible sister groups have been largely inconclusive. No obvious candidate has been found among other Cretaceous taxa but cladistic analysis suggests that they share a common ancestor with the Comasteridae among the comatulids. However, as with many other comatulids, comasterids have a poor fossil record and it is only the existence of *Marsupites* and *Uintacrinus* that establishes the presence of the Comasteridae as far back as the Late Cretaceous. Assuming, therefore, that the marsupitids arose from *Comatulella*-like comasterids during the Santonian (Late Cretaceous), it remains to be explained how and why their aberrant morphology developed.

Of the two, *Uintacrinus* has a less derived morphology than that of *Marsupites*. With one exception, this is based on degree of development rather than simple presence or absence of characters. In *Uintacrinus socialis*, the earliest of three marsupitid species, the thecal plates are smooth and the radials are comparable in size to the brachials in other comatulids. Infrabasals, or plates at the base of the cup interpreted as such, are present in only about half of the individuals (Springer 1901), and in all cases are very much smaller than the other thecal plates. In contrast, the thecal plates of *Marsupites* are all very much larger than the brachials, often have their surfaces heavily ornamented with radiating ridges, and plates interpreted as infrabasals are always well developed. Although the presence of infrabasals is actually apomorphic for articulates as a whole, their reappearance in *Marsupites* and *Uintacrinus* is a derived condition by comparison with other comatulids.

The aberrant morphology of these two genera is the reason why they have so often been classified erroneously. It also raises the question of how such an apparently bizarre morphology could evolve from 'normal' comatulids. The key to this, perhaps, lies in the ontogeny of certain comasterids. Immature examples of genera such as *Comatula* and *Comaster* have well-developed cirri on the centrodorsal but, in mature and gerontic individuals, the cirri are lost and the centrodorsal reduced to a small smooth plate. Adult comatulids also lack basals and infrabasals, but these are present early in the ontogeny of comatulids. The three-circlet arrangement of thecal plates in these taxa would, therefore, appear to be a juvenile trait, whereas the form of the centrodorsal, its lack of cirri, and also the shape of the brachials would, by comparison with comasterids and other articulates, appear to be extreme gerontic traits.

In conclusion, *Marsupites* and *Uintacrinus* appear to show, to differing degrees, a combination of heterochronic traits. On the one hand, there are features which recall the early ontogeny of comasterids, while, on the other, there is a series of extreme peramorphic traits which have carried the morphology of the two taxa well beyond the morphology of the adult comasterid.

GEOGRAPHICAL, STRATIGRAPHICAL AND FACIES DISTRIBUTIONS

The geographical distribution of *Marsupites* has been reviewed by Sieverts (1927) and Rasmussen (1961), and of *Uintacrinus* by Rasmussen (1961). Both genera have a cosmopolitan distribution, occurring on the continents of North America, Europe, Asia (including India), Africa and Australia. *U. socialis* and *M. testudinarius* are only known with certainty from the Upper Santonian.

Most of these crinoids are found in chalks, which are extensively developed in the Upper Santonian, although there are also records from marls and sandstones. Many of the older records give little detail of lithology. It is possible to show in Northern Ireland that the species occur only in chalks and are absent in co-eval glauconitic sandstones and other facies (Wilson and Manning 1978). Similarly, in Picardie in northern France, *Marsupites* is absent from lenses of granular phosphorite, but present in laterally equivalent chalks (Jarvis 1980). Pechersky *et al.* (1983) summarized records of *Marsupites* in calcareous facies (mainly chalks) of the Crimea, Caucasus and Kopet Dag, and contrasted these occurrences with the absence of the genus in clays and glauconitic sandstones to the north, on the Russian Platform. *Marsupites*, however, is present in sandstones at Plymouth Bluff in Mississippi, where it occurs rarely in a single 50 mm bed. It can be concluded that the distribution of *Marsupites* and *Uintacrinus* is controlled by the nature of the substrate, with a strong predilection for chalks, from which it may be inferred that they were benthic.

M. testudinarius (above) and *U. socialis* (below) occur in the Upper Santonian, with or without a short overlap of range. *U. anglicus* occurs only in England and succeeds *Marsupites*; it is best considered to be of earliest Campanian age. Besairie (1936) claimed that the *Marsupites* occurrence in Madagascar is of Campanian age. This appears to be improbable in view of its Santonian age elsewhere.

TAPHONOMY

Springer (1901) gave a detailed account of the occurrence and mode of preservation of the large groups of intact *Uintacrinus socialis* in the Niobrara Chalk of Kansas. Uintacrinids occur in the upper part of the chalk in lenticular deposits, only 25 mm thick in the centre. They generally cover a few square metres, although the largest outcrop recorded covered an area of more than ninety square metres (Springer 1901). In all circumstances, it is the lower surface of the slabs which displays the articulated crinoid remains, whereas the upper surface is covered with disarticulated ossicles. The junction between the crinoidal layer, and the much softer underlying and overlying chalk is very sharp, whilst the sediment component in the crinoidal layer is negligible. The differential preservation between the upper and lower surfaces, and the lack of the interstitial sediments, is very similar to that seen in the pseudoplanktonic pentacrinitids (Simms 1986). After the death of a colony, current action winnows and sorts the exposed material, whilst the lower surface is protected.

Grinell (1876) observed that in the Kansas material uintacrinid calyces lie flattened-out, usually on their sides. Specimens with the basal plates visible are not uncommon, but the upper portions of the uintacrinid calyx are never shown. Springer (1901) also noted that the most common calyx orientation was lying on its side. However, he stated that many were embedded base downwards, leaving the basal plates exposed on the lower slab surface; calyces preserved with the ventral surface orientated downwards were rare. Similar orientations are observed for *Marsupites* from the Santonian Chalk of Bridlington, Yorkshire. This indicates that the *Marsupites* and *Uintacrinus* were orientated with the oral surface facing upwards.

FUNCTIONAL MORPHOLOGY

Three mechanisms might be envisaged by which *Marsupites* and *Uintacrinus* could achieve a pelagic mode of life; passively through reduction in weight of the skeletal plates and generation of buoyancy by means of oil or gas; actively by swimming continually to maintain lift; or by attaching themselves to some independently floating material and becoming pseudoplanktic.

Structure of the ossicles

The absence of any means of attachment, such as a stem, indicates that *Marsupites* and *Uintacrinus* were free living. According to Bather (1896), Springer (1901) and Rasmussen (1961), the plates of both genera are extremely thin and fragile. However, the ossicles of specimens from the Upper Santonian of Britain are extremely robust and heavily calcified. These differences in mechanical properties of the plates may arise from differences in diagenetic alteration. Ossicles from the Niobrara Chalk, Kansas, have been subjected to diagenetic dissolution and subsequent micritization (Neugebauer 1978).

The thecal plates and robust, heavily calcified brachials of *Marsupites* and *Uintacrinus* do not show evidence of skeletal lightening. By contrast, the brachials of pelagic roveacrinids are often hollow and reduced to the minimum weight.

Nektonic potential

The endoskeleton of *Marsupites* and *Uintacrinus* is composed of high magnesium calcite, the density of which is significantly greater than that of sea water. The soft tissue component would also have been denser than sea water. Therefore, if *Marsupites* and *Uintacrinus* were pelagic, they must have either been continuously active in order to generate lift, or they must have possessed a special buoyancy mechanism. Effective swimming motion in crinoids is generated from the basal half of the arm (Shaw and Fontaine 1990). The critical articulation occurs between the radial facet and IBr_1, where the muscles that flex during the recovery stroke and the ligaments that contract during the power stroke are concentrated. Thus, the articular facet of the comatulids and nektonic roveacrinids dominates the radial plates. Reconstructions using fossil material have shown that the nektonic roveacrinids were capable of sweeping their arms through extensive arcs. *Hyalocrinus* from the Lower Cretaceous Gault of Folkestone, Kent, was capable of moving its arms through 105° (Griffiths 1989).

Mobility in *Marsupites* and *Uintacrinus* is severely restricted, due to the incorporation of proximal brachials into the thecal structure. In *Marsupites*, where the radial plates may form the ventral margin of the calyx, the curved nature of the facet would restrict movement. In addition, the musculature on such facets was poorly developed. The fulcral ridge terminates abruptly before it reaches the facet margin, and the muscle and ligament fossae are relatively small.

Planktonic potential

Bather (1896) proposed that the calyces of *Marsupites* and *Uintacrinus* have been expanded to accommodate a buoyancy mechanism. If a low density material was present in the calyx, the crinoid would only be stable if the calyx were orientated with the ventral surface facing downwards. Gislén (cited in Peck 1955) stated that it would be difficult for a crinoid to catch sinking particles of food if it were orientated with the mouth down.

Orientation

Bather (1896) suggested that *Marsupites* and *Uintacrinus* were orientated with the mouth directed upwards and were stabilized by strongly recurved arms that acted as a counterweight. In such an orientation, it might be anticipated that the thecal plates would be thickened dorsally. This would lower the centre of gravity and thus increase stability. However, the thecal plates are all of equal thickness.

MODE OF LIFE

Previous work

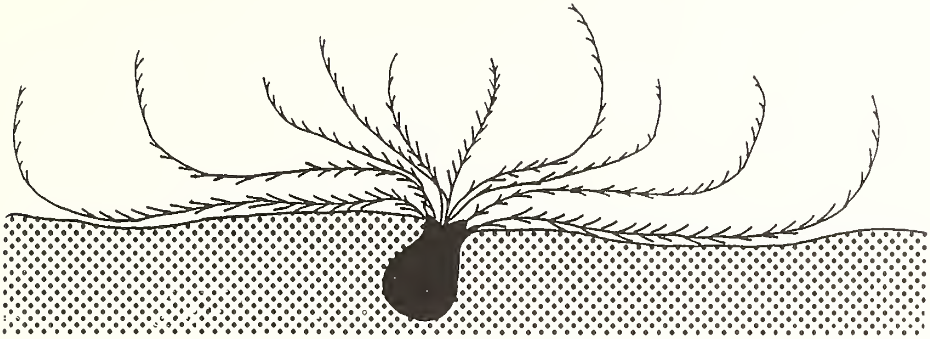
A planktonic mode of life for *Marsupites* and *Uintacrinus* was first proposed by Bather (1896). He based his conclusions on the presence of a light flexible calyx, long movable arms, and the absence of any means of attachment. Jaekel (quoted in Bather 1896) had suggested that *Saccocoma* may have been lightened by a slight development of gas within the theca. Bather implied that such a buoyancy aid may have also existed in *Marsupites* and *Uintacrinus*. He concluded that *Uintacrinus socialis*, which dominates in the Niobrara Chalk of Kansas, was pelagic and lived in swarms. However, as the European species *U. westphalis* occurs as isolated specimens, Bather (1896) designated it pelagic, but not gregarious.

Springer (1901) also concluded that *Uintacrinus socialis* was pelagic. He envisaged the crinoids swimming together in schools aided by their long and powerful arms. He suggested that specimens may have become entangled when there was no suitable site of attachment available, as occurs in antedons (Carpenter 1866). Springer thus indirectly suggested that these schools were usually pseudopelagic, presumably attached to a float by their arms. A pseudopelagic mode of life was also proposed by Schuchert (1904). He suggested that *Uintacrinus socialis* may have held itself to foreign objects by its long slender arms.

Proposed mode of life

The heavily calcified endoskeleton of *Marsupites* and *Uintacrinus* is not indicative of a pelagic mode of life. The presence of a buoyancy mechanism is discounted because the thecal volume has not been expanded and is proportional to arm length. Also, if such a mechanism were present, the crinoid would only be stable if it was orientated with the oral surface facing downwards. This contradicts the taphonomic and morphological evidence which indicates that *Marsupites* and *Uintacrinus* were orientated with the oral surface upwards. Limited flexibility in the proximal arm section, and the weakly developed musculature of the brachials, indicates that they were unable to swim and were not therefore nektonic. Finally, there is no direct evidence, in the form of associated driftwood or similar substrate, for a pseudoplanktonic mode of life.

We propose that *Marsupites* and *Uintacrinus* lay on the sea floor with the calyx embedded in the sediment (Text-fig. 3). The proximal sections of the arms lay on the sediment surface, stabilizing the crinoid, whilst the distal ends curved upwards to form a feeding bowl. The distal section of the arms was flexible so that when a slight current was present, the arms could be orientated with the aboral surface facing down-current to increase the feeding efficiency, as observed by Meyer (1973) in the comatulids. However, such rheophobic feeding is extremely rare in extant crinoids. Meyer (1973) states that deep sea species of comatulids may be rheophobic, but the collecting bowl is only a temporary feeding method employed when currents are slack.



TEXT-FIG. 3. Proposed mode of life for *Uintacrinus* and *Marsupites*; stipple represents sea bed sediments.

The crinoids may have been mobile. It is possible that they were able to move across the substrate by repeated extension and contraction of the pinnules in the distal parts of their long arms. Shaw and Fontaine (1990) demonstrated that crawling in comatulids involves the distal arm section and loss of only twenty per cent of the arm limits crawling activity. When extended, the pinnules would produce a larger surface area to 'push off' from, and as the arm lifted away from the substrate, flattening the pinnules against the main arm axis, drag would have been minimized. However, the heavily calcified endoskeleton and weakly developed musculature would have limited such activity.

The world-wide distribution of *Marsupites* and *Uintacrinus* probably reflects a plankotrophic larval stage. Such larvae are able to subsist on planktic food, which allows a long larval duration (Jablonski and Lutz 1983) and hence high dispersal capability. Thorson (1950) estimated that seventy per cent of all benthic marine species undergo planktotrophic development. In temperate-water species, this planktic stage generally lasts from two to six weeks (Thorson 1961), allowing for a dispersion of 150–550 km in a current of only 0·5 km/hr (Scheltema 1977). However, tropical benthos may remain as plankton for up to six months and thus may be carried great distances by ocean currents.

CONCLUSIONS

Phylogenetic analysis reveals that *Marsupites* and *Uintacrinus* are united in a single clade, the Marsupitidae, whose sister taxon is the Comasteridae. Functional analysis of their morphology indicates that *Marsupites* and *Uintacrinus* were benthic. We propose that they lay on the sea floor with the calyx embedded in the sediment. The proximal section of the arms provided support, whilst the distal arm sections formed a feeding bowl. The world-wide distribution of *Marsupites* and *Uintacrinus* probably reflects a long larval stage.

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ELECTRORECEPTORS IN THE LOWER PERMIAN TETRAPOD *DISCOSAURISCUS AUSTRIACUS*

by J. KLEMBARA

ABSTRACT. In most ornamented dermal cranial bones of the larvae of the Lower Permian tetrapod *Discosauriscus austriacus* from Moravia, distinct rounded or oval pits are present. They are situated in, or close to, the sensory grooves and pit-lines. The diameter of each pit is *c*. 1 mm. The inner surface is sometimes smooth and consists mainly of smaller pits, depressions, or short canals which have small foramina at their bases. Such structures, designated as foraminate pits, have not previously been found in tetrapods. Positionally and structurally, the foraminate pits are comparable with the so-called pore-groups of some rhipidistians, in particular the osteolepids. It is concluded here that these structures are homologous and that the bones which bear them must therefore also be homologous. Thus the bones enclosing the pineal foramen in osteolepiforms are frontals. On the basis of comparisons with Recent urodeles, the foraminate pits are interpreted as structures which may have housed the ampullary electroreceptive organs. If so, *Discosauriscus*, like the rhipidistians, was an electroreceptive animal.

As reported elsewhere (Klembara 1992, 1993, 1994; Klembara and Meszároš 1992; Klembara and Janiga 1993) the Lower Permian localities in the Boskovice Furrow in Moravia (Czech Republic) have produced well preserved three-dimensional material of the tetrapod *Discosauriscus austriacus* (Makowsky, 1876). The most recent finds are of large specimens, and smaller individuals with external gills, showing that *Discosauriscus* is represented by larval and metamorphic individuals (Klembara, in press a). The material reveals many detailed structures. The pit structures, already briefly reported as foraminal pits (Klembara 1992), occur in constant positions in dermal cranial bones, always in relation to the sensory line system. They have not previously been recorded either in early tetrapods ('stegocephalians') or in Recent ones. In this paper, specimens of *Discosauriscus* with skull lengths in the range 17–52 mm are considered.

The term 'Rhipidistia' is used *sensu* Jarvik (1980, p. 202) in this work. The term 'orthodox' terminology, as applied to dermal cranial bones of osteolepiforms, is used here in the sense of Westoll (1943; cf. Borgen 1983); according to this terminology, the bones which enclose the pineal foramen in osteolepiforms are frontals.

MATERIAL, METHODS AND LOCALITIES

The methods of study and the localities for *Discosauriscus austriacus* from the Lower Permian of the Boskovice Furrow were described by Klembara and Meszároš (1992). A third and new locality lies about 500 m northeast of Kochov (district of Letovice). Abbreviations for the localities are: D, Vanovice (Drválovice); K, Kochov; KO, Kochov-L.

The foraminate pits occur on the bones of following specimens which are deposited in the Faculty of Natural Sciences, Zoological Institute, Comenius University, Bratislava: premaxillary, D54, D91; nasal, K224, K327; prefrontal, K80; frontal, K206, KO80, KO111; postfrontal, D47, D137, K3, K102, KO12; intertemporal, K57, K279; supratemporal, KO13, KO25; parietal, D3, D19, D43, D56, D70, D75, D192, D200.III, K13, K18, K20, K48, K63, K185, K205, K227, K231, K241, K316, K320, K325, KO10, KO41, KO60, KO63, KO80; postparietal, D3, D43, D48, D60, D63,

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D69, D75, D79, D82, D104, K3, K5, K13, K18, K63, K65, K98, K182, K185, K227, K256, K278, K279, K324, K325, K326, KO7, KO77; tabular, D72, D86, D87, D137, K241; K256, K325, K326, KO7, KO8, KO10, KO11, KO41; maxillary, K180, K257, K316; lacrimal, D54, D73, D81, K195, K328; jugal, K180, K325; squamosal, D53, K98, K256; dentary, D28, K257. Other specimens used: K60, K69, K172.

DESCRIPTION

On the external surface of most dermal cranial bones of *Discosauriscus austriacus*, pit structures – called the foraminate pits (FPs, *fossulae foraminosae*) (Klembara 1992) – are present. Such structures have been found in the premaxillary, prefrontal, nasal, frontal, postfrontal, intertemporal, supratemporal, parietal, postparietal, tabular, maxillary, lacrimal, jugal, squamosal and dentary.

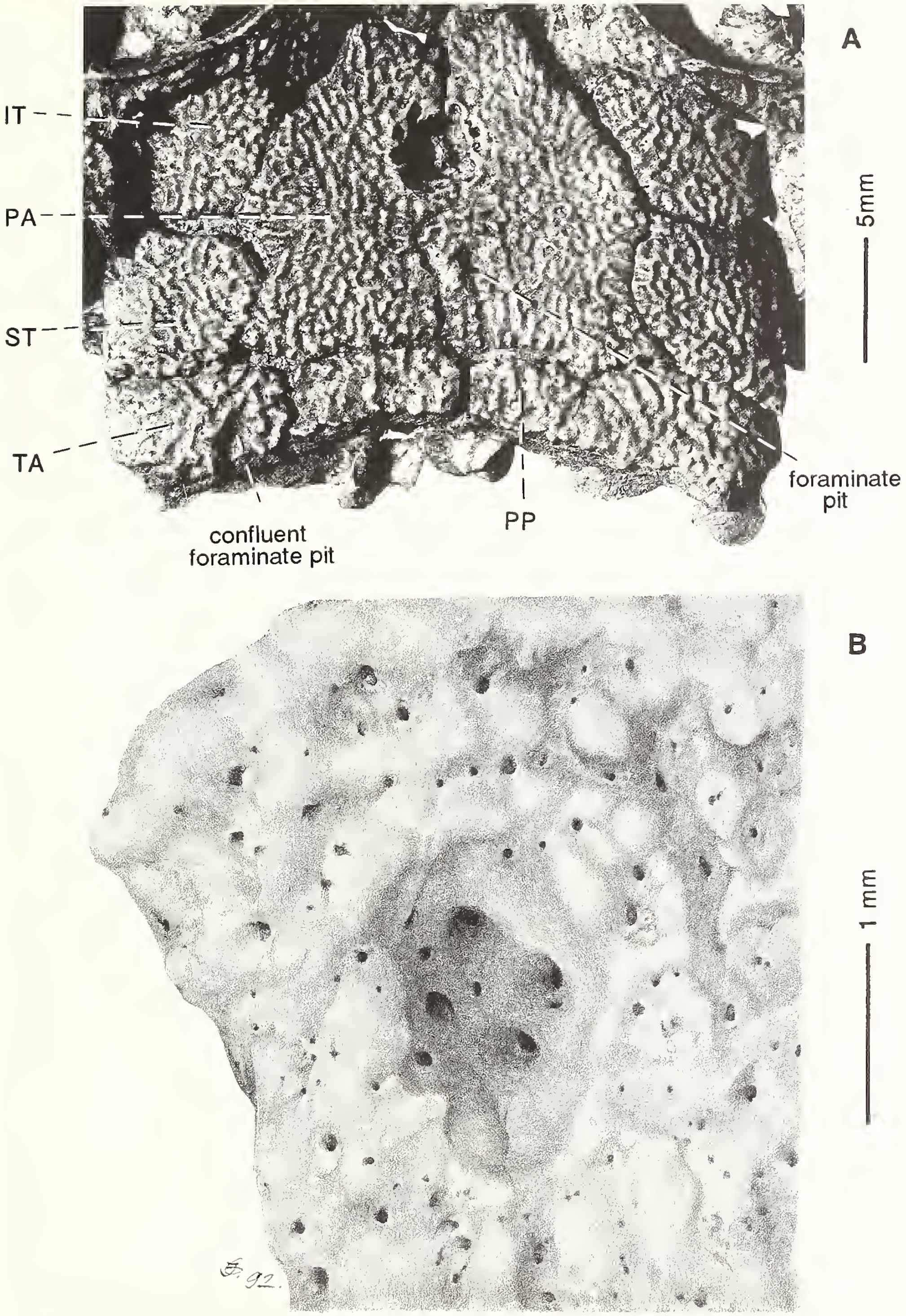
The FPs are generally round, oval or elliptical (Text-figs 1; 2B–C, E, G; 3A, C–E; 5; 6D; 7C–D; F; 8H–I). Their size does not depend on the size of the individual. They vary in depth and may be narrow and relatively deep (Text-fig. 1), or relatively wide and shallow (Text-fig. 6D). The diameter of the shallow and oval FPs may reach up to 1·3 mm, although most of them attain a maximum diameter of 1·0 mm.

The morphology of the inner surface of the FPs is not uniform, although there is a common basic structure. The inner structure of a typical FP is irregular and consists of smaller pit structures (depressions, short grooves, pits and vertical or oblique canals). These pit structures are of various sizes and shapes, and every pit has a tiny foramen (or pore) at its base, leading into the bone (Text-figs 1, 5). The number of foramina in one FP varies from two to ten (it is sometimes difficult to distinguish between a minute pit and the foramen), but there are usually four to seven foramina in one FP. The small pit structures lie mostly in the bottom and in the lower portion of the wall of the FP. However, they are not always clearly developed, so that in some specimens the foramina lie in the almost smooth inner surface of the FP (Text-figs 3A, C–D; 6B, D; 7C; 8H). On the other hand, in the FP of the right parietal of K241, short bulbous and funnel-shaped pits or canals are present, narrowing down into the bone. At the base of these structures, the tiny foramina are clearly visible. It should be emphasized that the morphology of the inner surface within one FP varies so that within a single FP, pits or depressions of various size, canals or foramina in the smooth surface may be simultaneously present (Text-fig. 5B). The location of foramina within the FP surface is irregular, although in K324, the inner surface of the right postparietal FP is relatively smooth and a ring of foramina lies in the basal portion of its wall (Text-fig. 7D; this is also seen in other specimens, such as the posterior FP of the left parietal of D75). The same structural variability seen in the FPs is also observable in the sensory grooves and pit-lines (Klembara 1992, in press b).

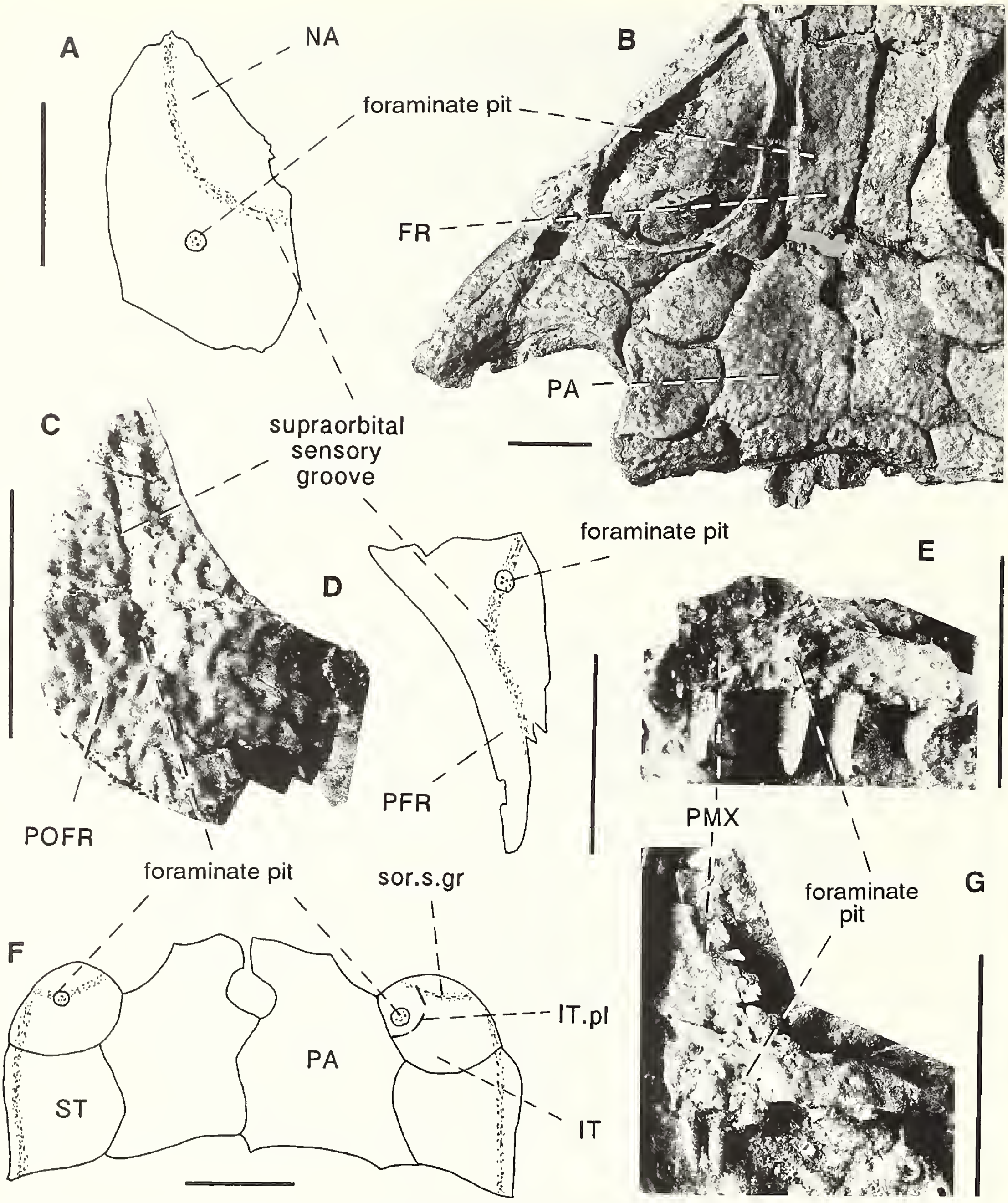
On the ventral surface of the bone, immediately below the FP, a foramen is present in some specimens (e.g. right postparietal of D75, left postparietals of K18 and K278, and left tabular of K256). Although it is probable that this foramen served for the passage of a nerve which ramified inside the bone into small branches passing through the foramina in the FP, this cannot be verified without information from histological sections (this is, however, difficult because the bones contain many relatively large cavities and canals). Because such foramina, like the FP, lie more or less in the central or posteromedial parts of bone in these specimens, the foramen could also be nutritive in function or serve for the nerve of the lateralis system. This is supported by the fact that in those specimens without FP's, foramina are present in the corresponding regions of the bones. An interesting condition is seen in K20, in which the FP lies in the posteriormost part of the right parietal which overlaps the unornamented area of the postparietal. On the ventral surface of this postparietal, there is a group of three foramina which may correspond to the group of foramina in the inner surface of the parietal FP (Text-figs 3A–B). The two groups of foramina do not coincide dorsoventrally; the ventral one is situated slightly more posteriorly. If both groups of foramina were functionally connected, this would imply that the nerve had ramified (at least in this specimen) before entering the bone.

There is usually one FP in each bone. The occurrence of two FPs in immediate proximity is rare (Text-figs 4G; 6A, C–D). In K227, the FP is mediolaterally prolonged. The distribution of foramina on the inner surface of this more or less elliptical depression suggests that it represents two confluent FPs (Text-fig. 5). Two more or less confluent FPs are present also in some left and right postparietals (Text-figs 4B; 6B; 7E (in which two pits are arranged in an anteroposterior orientation with the anterior pit extending slightly into the right parietal)) and in either left (Text-figs 1A; 4G; 7A) or right (Text-fig. 4H) tabulars.

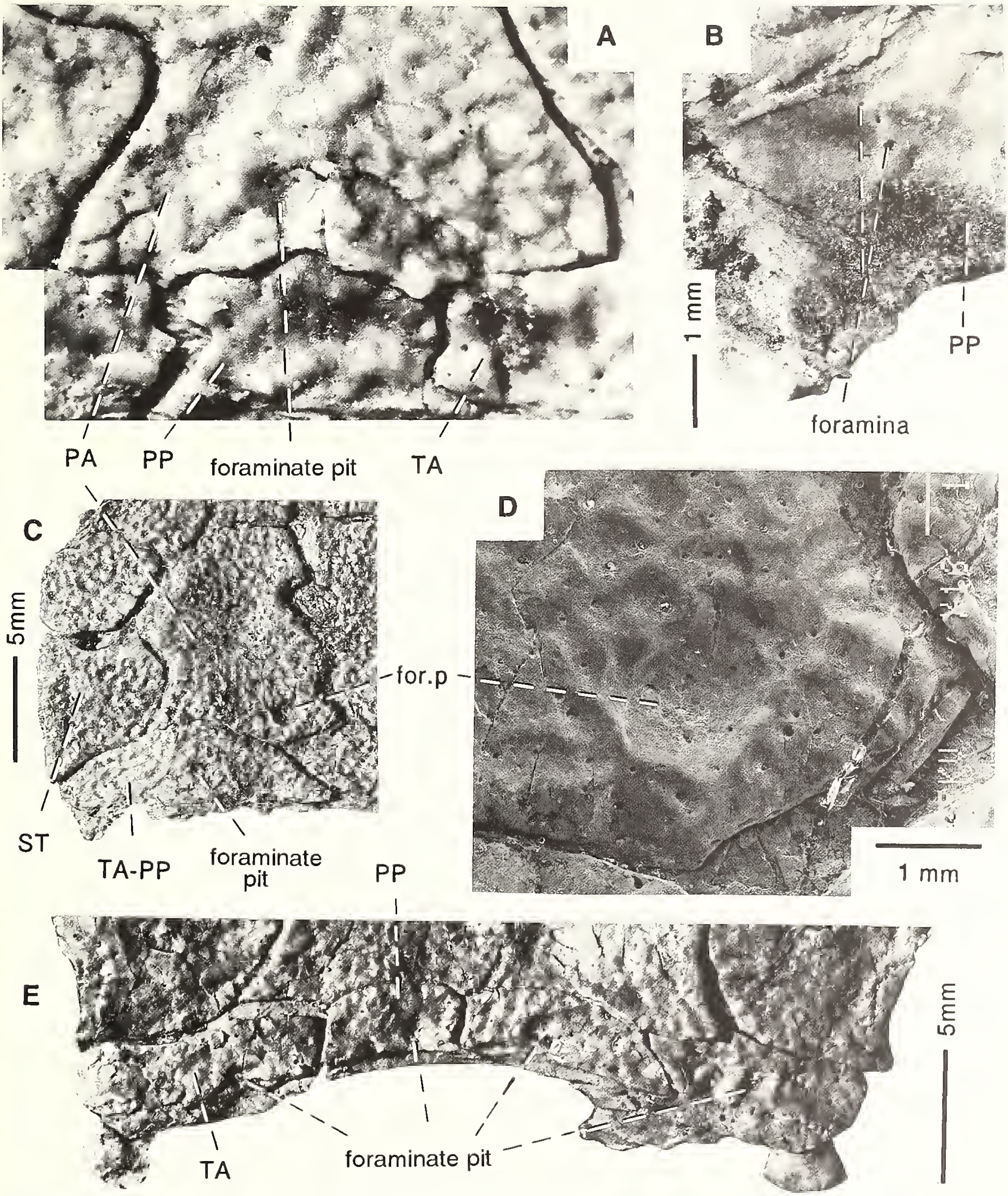
The FPs lie characteristically in or close to the sensory grooves and pit-lines (Text-figs 4E, 9). The lateral line system of *Discosauriscus* has been described elsewhere (Klembara 1992, in press b) and includes sensory grooves (or canals) and pit-lines (the first record in fossil amphibians). The FP also has a more or less constant position within the bone (see also Text-fig. 9).



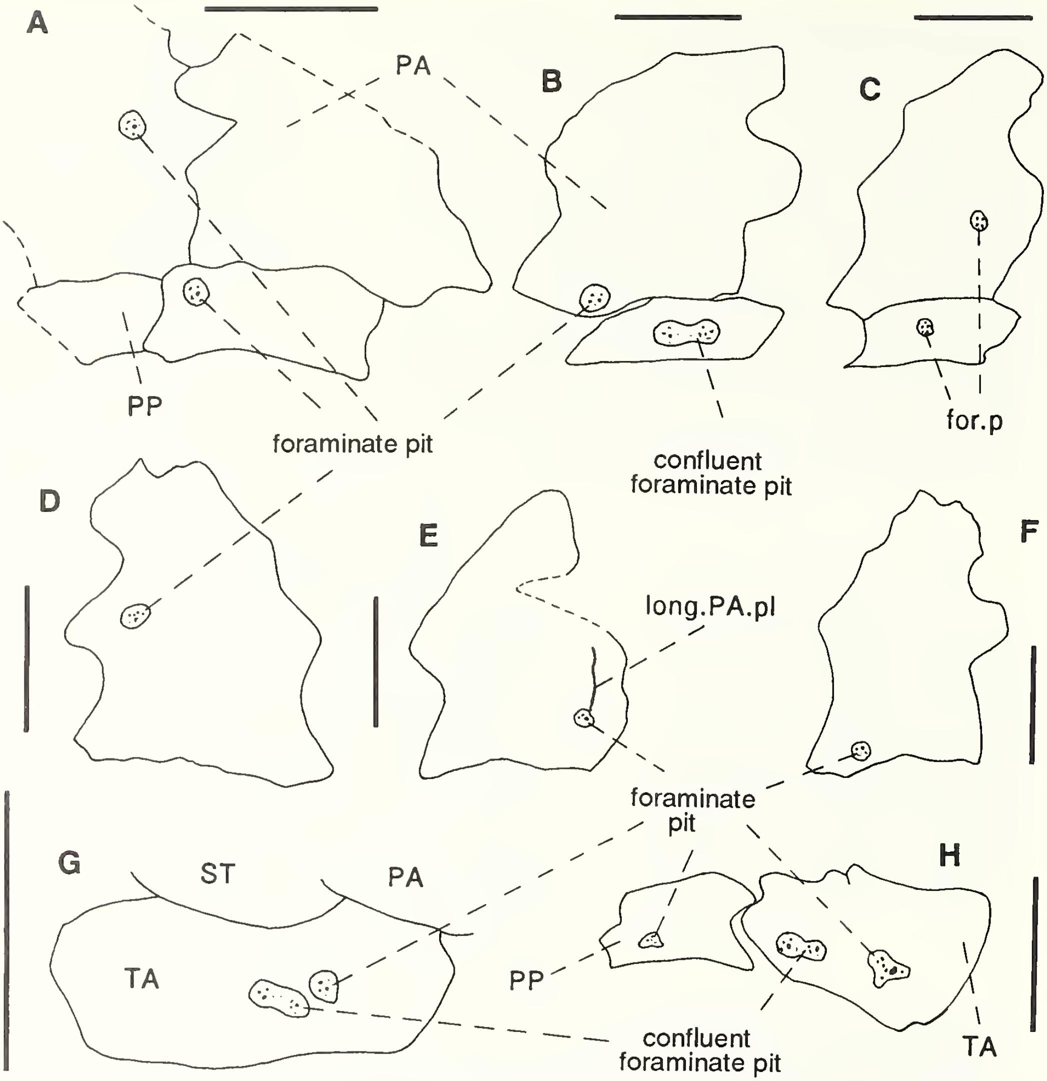
TEXT-FIG. 1. *Discosauriscus austriacus* (Makowsky); K241. A, posterior portion of skull table in dorsal view. B, illustration of enlarged foraminal pit of right parietal of the same specimen.



TEXT-FIG. 2. *Discosauriscus austriacus* (Makowsky). A, K224; right nasal. B, K206; skull roof. C, D47; right postfrontal. D, K80; left prefrontal. E, D54. G, D91; left premaxillaries. F, K57; posterior part of skull table. All figures in dorsal view. Scale bars represent 5 mm.



TEXT-FIG. 3. *Discosauriscus austriacus* (Makowsky). A, K20; foraminate pit in posterior part of right parietal. B, group of three foramina in ventral surface of right postparietal of the same specimen as 3A. C, D43; left side of posterior part of skull table. D, enlarged foraminate pit of left parietal of the same specimen as 3C. E, K326; foraminate pits in posteriormost bones of skull table. All figures in dorsal view except for 3B.



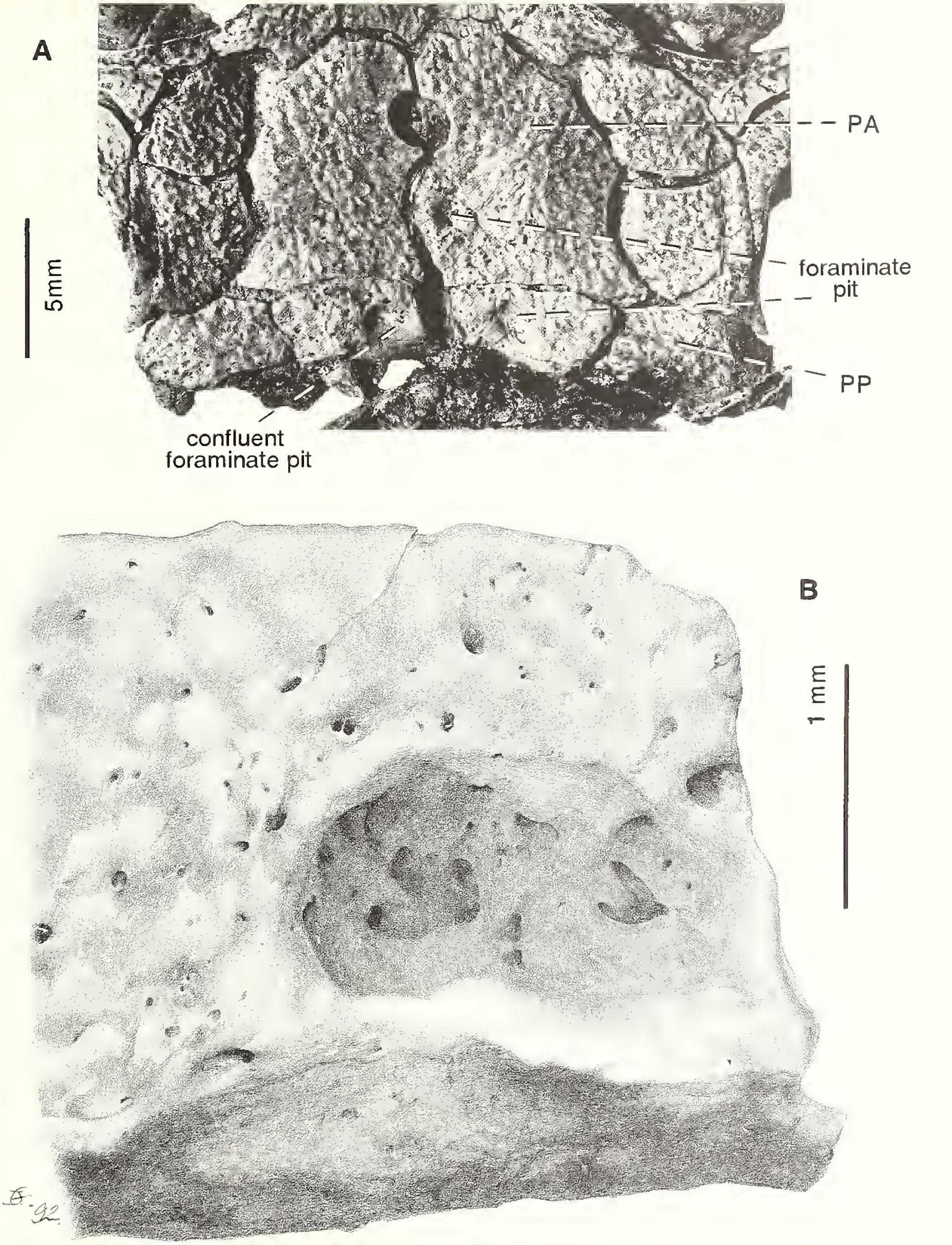
TEXT-FIG. 4. *Discosauriscus austriacus* (Makowsky); outlines of dorsal surfaces of some exocranial bones with foraminate pits. A, K185; parietals and postparietals. B, K63. C, K18; left parietals and postparietals. D, D70; right parietal. E, K231. F, D200.III; left parietals. G, D86; left tabular. H, KO7; right postparietal and tabular. Scale bars represent 5 mm.

Premaxillary. FPs are visible in two left premaxillaries (Text-fig. 2E, G). In both specimens, the FP lies very close to the junction of the infraorbital and supraorbital sensory grooves.

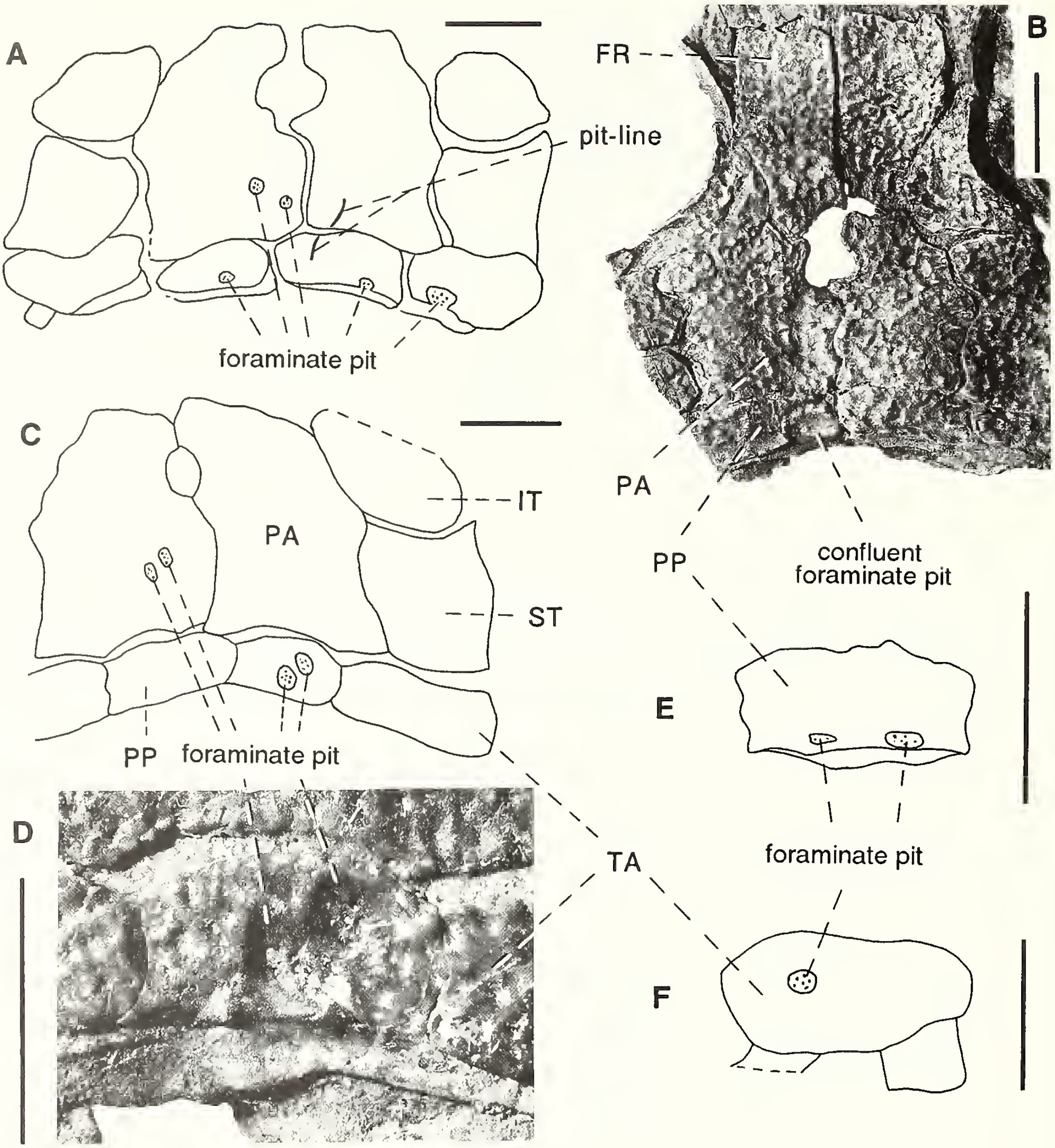
Nasal. In the nasals, the FP is situated close to the lacrimal section of the supraorbital sensory groove (Text-figs 2A, 9).

Prefrontal. A prefrontal FP was found only in the left prefrontal of K80. It lies directly on the path of the sensory groove (Text-fig. 2D).

Frontal. The FP in the left frontal of K206 is situated in the corner formed by the supraorbital sensory groove laterally and the anterolateral part of the frontal pit-line anteromedially (Text-fig. 2B). Although the frontal



TEXT-FIG. 5. *Discosauriscus austriacus* (Makowsky); K227. A, posterior part of skull roof in dorsal view; B, enlarged confluent foraminate pit in left postparietal of the same specimen.



TEXT-FIG. 6. *Discosauriscus austriacus* (Makowsky). A, K325; posterior part of skull table. B, D48; skull table. C, D75; partial posterior skull table. D, two foraminate pits of right postparietal of the same specimen as C. E, K5; right postparietal. F, KO8; right tabular. All figures in dorsal view. Scale bars represent 5 mm.

pit-line is absent in this specimen, its course is clearly visible in other specimens (e.g. K60, K69; see Klembara 1992, in press b). The FPs in K111 and KO80 are in similar positions.

Postfrontal. The FPs in the left and right postfrontals lie directly in the sensory groove (Text-fig. 2C; Klembara 1992, fig. 1B).

Intertemporal. FPs occur in the left intertemporals of K57 and K279. They are situated directly in the sensory grooves. The FP in the right intertemporal of K57 lies immediately medially to the intertemporal pit-line (Text-fig. 2F).

Supratemporal. The supratemporal FP of KO13 lies in the anteromedial portion of the right supratemporal, close to the supratemporal pit-line. In KO25, the FP lies directly in the posterior section of the postotic sensory groove of the right supratemporal (Text-fig. 9).

Parietal. Within the parietals, FPs occur in four basic positions.

(1) Immediately posterolaterally to the pineal foramen (Text-fig. 4A, D).
(2) Mid-way between the pineal foramen and the posterior margin of the bone (Text-figs 1, 4C, 5).
(3) Slightly anterior to the posterior margin of the bone (Text-figs 3A, C–D, 4E).
(4) In the region of the posterolateral corner of the bone (Text-fig. 4B, F).

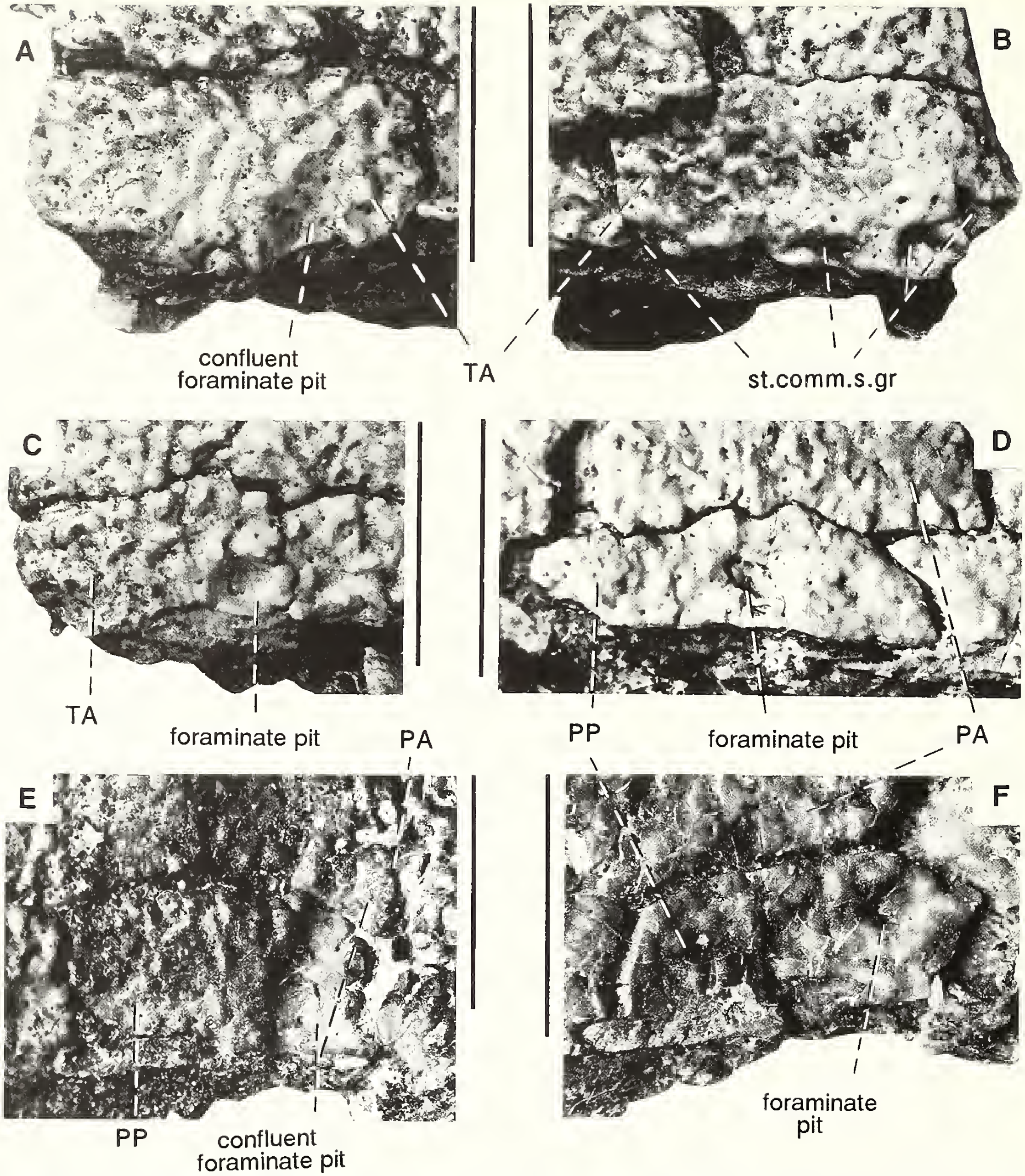
In the first three positions (and sometimes in more or less intermediate positions), the FPs always lie in the close vicinity of the median suture and directly in, or close to, the parietal pit-lines (Text-fig. 9). The FPs situated in the posterlateral corner of the parietal are approximately equidistant between the oblique (and/or theoretically transverse) parietal pit-lines and the supratemporal commissural sensory groove. As already mentioned, a pair of FPs sometimes occurs in the posterior portion of one parietal (Text-fig. 6A, C).

Postparietal. Most of the postparietal FPs are concentrated in the central and posteromedial portion of the ornamented part of the bone, directly in, or close to, the supratemporal commissural sensory groove or postparietal pit-lines (Text-figs 3E, 4H, 5A, 6A, 7D). More rarely, the FP lies in the anterior portion of the postparietal (Text-figs 4A, 7F). In D43, the left postparietal and tabular are fused as one element and here the FP lies in the lateral region of the postparietal component of this tabulo-postparietal (Text-fig. 3C). The FP in the left postparietal of K182 is in a similar position. In D75, one of the FPs in the right postparietal, lies in its anterolateral region (Text-fig. 6C–D). As already mentioned, in the left postparietals of K63, K227, D3 and D48 and in the right postparietal of K3, a pair of partly confluent PFs occurs (Text-figs 4B, 5, 6B, 7E). In the right postparietal of K5, two FPs are present (Text-fig. 6E): the lateral one lies in the posterolateral corner while the second, smaller FP lies in the medial half of the bone. The structure of these two FPs, together with those in the right postparietal of K324 (Text-fig. 7D) and in the left postparietal of D60 (Klembara, in press b), is very similar: elliptical shape, steep, distinct wall and relatively smooth bottom surface. In K5 and K324, the foramina are situated in the basal portions of the wall of FPs.

Tabular. Like most of the postparietal FPs, the tabular FPs are situated in the central, medial or posteromedial portion of the ornamented part of bone (Text-figs 3E, 4G, 6A, 7C), i.e. directly in or close to the supratemporal commissural sensory groove. There are exceptions to this. The FP in KO8 lies in the anteromedial part of the right tabular (Text-fig. 6F). The left tabular of D86 and the right tabular of KO7 bear two FPs. In both specimens, the left FP is confluent (Text-fig. 4G–H). Two almost confluent FPs are in the left tabular of K241 (Text-figs 1A, 7A).

The posterior margin of the ornamented surfaces of the tabulars and postparietals in most specimens of *Discosauriscus* are irregular and relatively large foramina occur in them. They are generally situated in the posterolateral corners of the tabulars (Text-fig. 7B) but they are also present in other regions of the ornamented skull table posterior margin. These pits are smaller than the FPs and usually have one foramen at the base. They formed a part of the supratemporal commissural sensory groove which ran along the posterior ornamented margin of the skull table and they are morphologically comparable to similar pits occurring in the floors of the sensory canals in other regions of the skull. Therefore, although distinction is sometimes difficult, these pits should not be misinterpreted as the FPs lying directly or very close to the supratemporal commissural sensory groove.

Maxillary. In the anterior part of the right maxillary of K316, one relatively small and deep FP is present (Text-fig. 8B). It is situated close to the lacrimal section of the infraorbital sensory groove. The FP in the left maxillary of K180 is in the same position. In the right maxillary of K257, a typical (more shallow) FP is present (Text-fig. 8A), and lies a little more anteriorly and closer to the tooth row in comparison with the FPs of K316 and K180.



TEXT-FIG. 7. *Discosauriscus austriacus* (Makowsky). A, K241; left tabular (cf. Text-fig. 1A). B, K172; right tabular. C, K256; left tabular. D, K324; right postparietal. E, D3; left postparietal. F, D104; left postparietal. All figures in dorsal view. Scale bars represent 5 mm.

Lacrimal. In the right lacrimals of K195 and D81, round and deep FPs are present. They lie close to the lacrimal section of the infraorbital sensory groove (Text-fig. 9). In the left lacrimals of D54 and D73, the FP lies in the anteriormost part of the lacrimal section of the infraorbital sensory groove (Text-fig. 8C) and in the left lacrimal of K328, the FP lies in its posterior part.

Jugal. Two closely spaced FPs are present in the right jugal of K325 (Text-fig. 8I). The more medial one is situated at the point where the jugal and infraorbital sensory grooves meet; the more lateral one is situated on the jugal section of the infraorbital sensory groove. An FP in the left jugal of K180 also occurs in the latter position (Text-fig. 8G).

Squamosal. In the right squamosal of K256, two closely spaced FPs are present (Text-fig. 8H); the more anterior one is smaller, the posterior one is larger. This pair of FPs lies in the area of the squamosal section of the jugal sensory groove. Single FPs in the right (Text-fig. 8F) and in the left (D53) squamosals are situated in similar positions.

Dentary. One deep FP is present midway along the right dentary of D28 (Text-fig. 8D). In the anterior parts of both dentaries of K257 two FPs are situated respectively. The FP in the left dentary is prolonged and probably represents two confluent FPs (Text-fig. 8E).

COMPARISON AND DISCUSSION

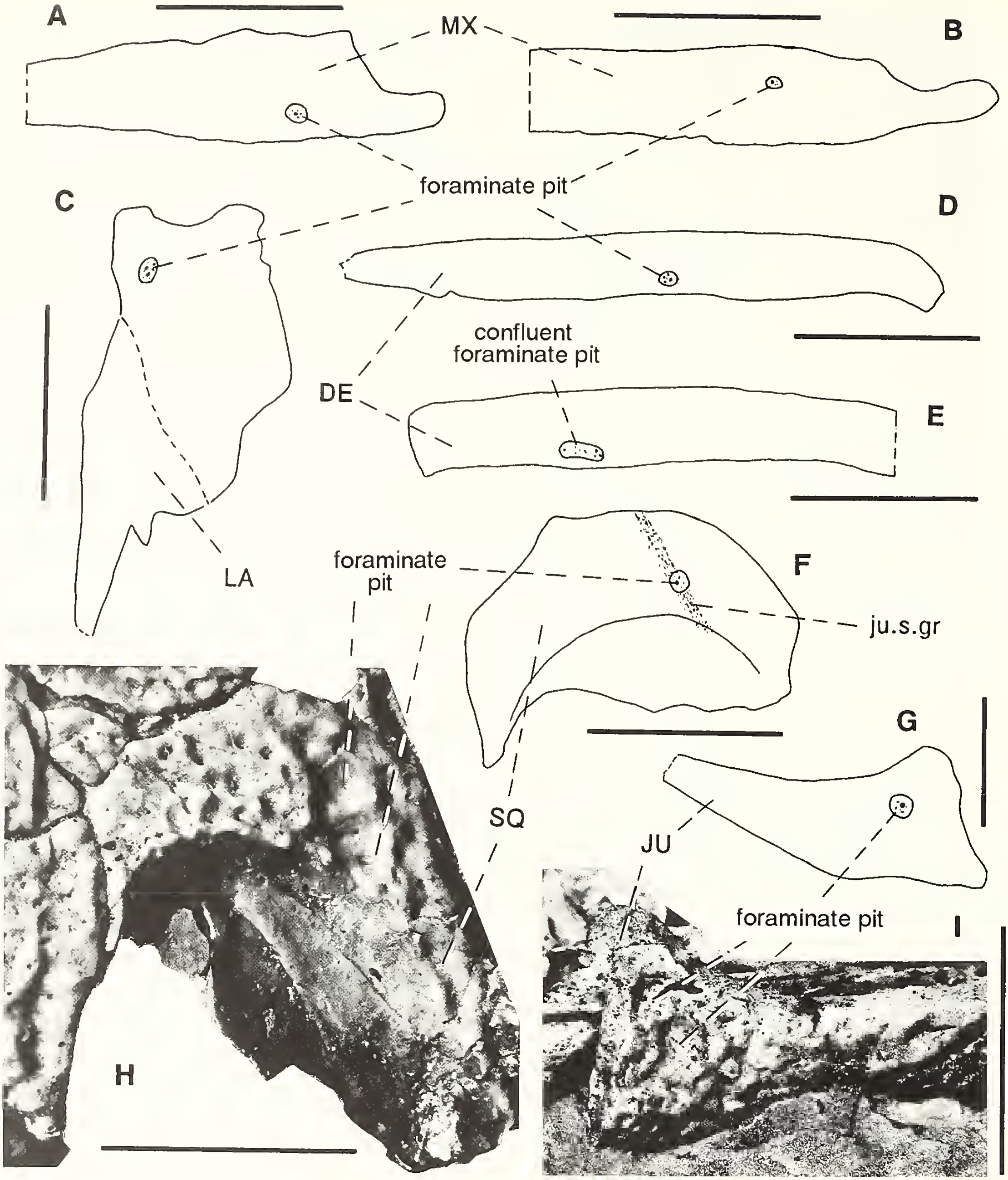
Because the FPs described above have not been previously recorded in fossil or in Recent tetrapods, it has been necessary to search for corresponding structures in fishes. Among them, two types of similar structure occur. These are: (1) the so-called pore-groups found in rhipidistians; and (2) the groups of cranial pits found in arthrodires. In both cases, as in *Discosauriscus*, they comprise distinct groups of foramina lying close to one another.

Pore-groups

The pore-groups, first described by Jarvik (1948) in Devonian osteolepids, are the groups of small pores found on the external faces of some dermal cranial bones. Such distinct groups of small foramina have been found subsequently in various rhipidistians (Gross 1956; Ørvig 1960, 1961; Jessen 1966, 1975, 1980; Bjerring 1972; Chang 1982; see also 'cutaneous sense organs' of Ørvig 1961). In rhipidistians, they occur mostly within the frontoethmoidal shield but also in some bones of the cheek, mandible and branchiostegal rays. The posteriormost occurrence of pore-groups within the dorsal portion of the skull roof is in the intertemporal (Jessen 1966; Bjerring 1972). The common characteristic of the pore-groups is that they are 'usually well defined and distinct, but the parts of the external faces of the dermal bones that bear these groups are generally neither depressed nor elevated' (Jarvik 1948, p. 137). However, Bjerring (1972) recorded the intertemporal groups of pores situated in a shallow depression in one Carboniferous osteolepiform and Jessen (1966, p. 318) found that the pore-group in the anterior supraorbital 'lies distinctly slightly immersed relative to the outer surface of the surrounded cosmine layer'. The pore-groups are situated close to the sensory canals or pit-lines. Bjerring (1972, p. 85) proved that the foramina of the pore-group 'are the upper extremities of a narrow, dorsally branching canal which passes obliquely through the intertemporal and opens to the surface of the bone somewhat mesial to the longitudinal row of nerve openings leading into the lateral-line canal system'.

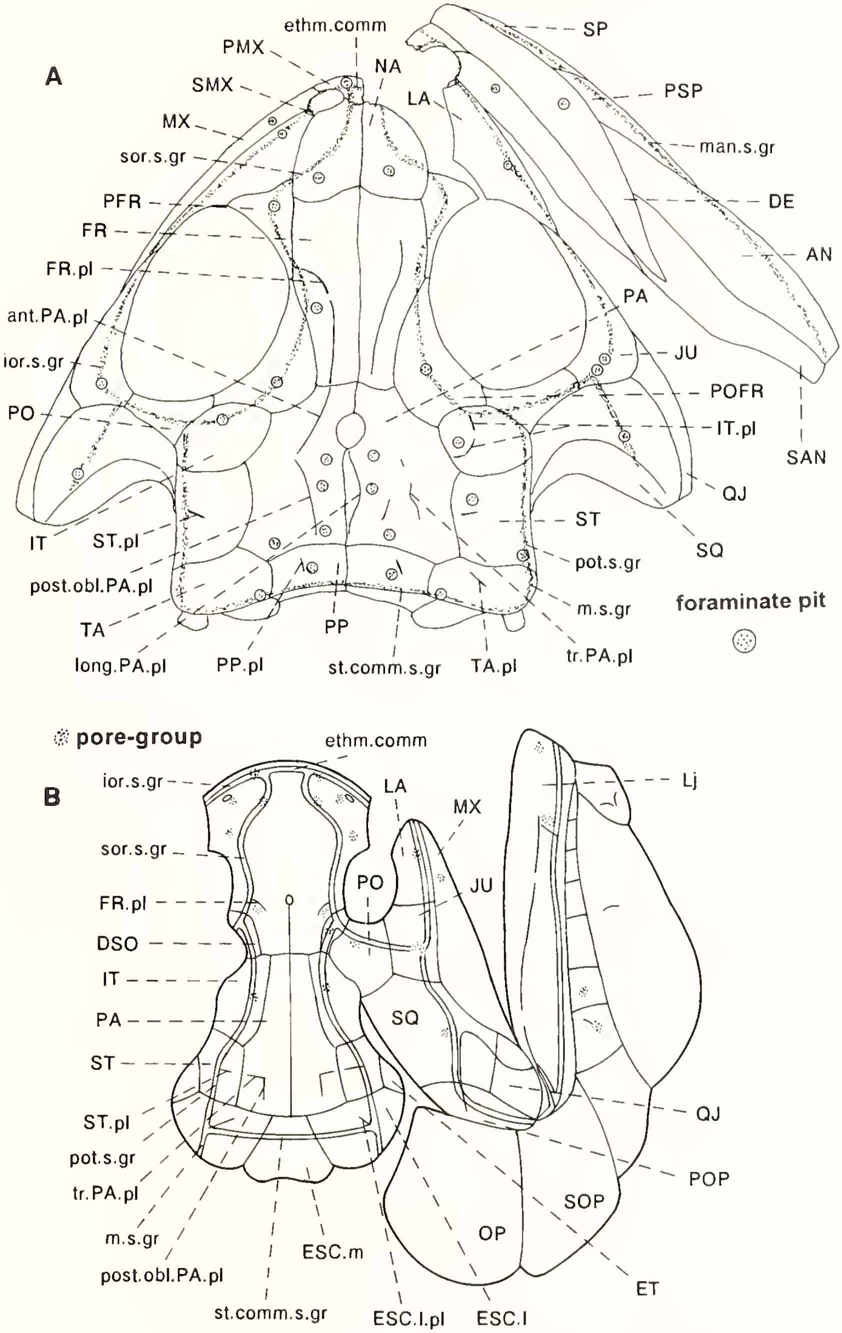
Comparison of the pore-groups of rhipidistians with the FPs of *Discosauriscus* shows striking positional and morphological similarities of both structures.

(1) The groups of foramina form distinct patches.
(2) The size (the diameter) of the FP corresponds to the size of the pore-group (always in relation to the size of the skull).
(3) The corresponding number of foramina in one group: Bjerring (1972) recorded intertemporal pore-groups of eight (left) and seven (right) foramina; in *Discosauriscus* the number of foramina in one FP varies from two to ten.



TEXT-FIG. 8. *Discosauriscus austriacus* (Makowsky). A, K257; right maxillary. B, K316; right maxillary. C, D54; left lacrimal. D, D28; right dentary. E, K257; left dentary. F, K98; right squamosal. H, K256; right squamosal. G, K180; left jugal. I, K325; right jugal. All figures in dorsal view. Scale bars represent 5 mm.

(4) Only one or two (independent or confluent), exceptionally three (Text-fig. 4G–H) or probably more (Jarvik 1948, fig. 68B) distinct groups of foramina have been observed in one bone. This is, however, judged in the rostral portion of the frontoethmoidal shield in fishes where the bones



TEXT-FIG. 9. A, *Discosauriscus* skull roof (dorsoventrally pressed) showing position of sensory grooves, pit-lines and foraminate pits (based on Klembara 1992, in press b). B, pore-groups, sensory canals and pit-lines observed in exocranial bones of osteolepids from the Middle Devonian of Scotland; combined from several specimens (after Jarvik 1948, fig. 36A); pore-groups in dermosphenotic, intertemporals, maxillary and right lateral extratemporal pit-line based on the Devonian osteolepid *Latvius* (Jessen 1966, fig. 1B–C).

are mostly fused. In all cases, the groups of foramina lie at certain distances to one another and they are not aggregated in larger concentrations in one bone as in arthrodires (see below).

(5) The presence of two closely spaced groups of foramina (Jarvik 1948, fig. 22F in the right squamosal and in the right squamosal of *Discosauriscus*; Text-fig. 8H) or of two confluent groups of foramina (Jarvik 1948, fig. 23E in the lower jaw; Text-figure 8E).

(6) The groups of foramina are situated close to the sensory canals and pit-lines. In *Discosauriscus*, the FPs sometimes lie directly in the sensory grooves (Text-fig. 9A) because the latter, contrary to the situation in fishes, lie on the bone surface. However, as seen in osteolepids (Text-fig. 9B), some pore-groups lie directly above the sensory canals.

(7) The striking position similarity of individual groups of foramina.

  (a) The premaxillary FPs lie in the region of the junction of infraorbital and supraorbital canals (Text-fig. 2E, G) exactly like the pore-groups of the premaxillary region in osteolepids (Jarvik 1948, fig. 36A), *Powichthys* (Jessen 1975, figs 1D, 2) and *Youngolepis* (Chang 1982, figs 5B, 6C); see also Text-figure 9.

  (b) The position of nasal FPs (Text-fig. 2A) corresponds well to the position of pore-groups in the region of the nasals and postrostrals in osteolepids (Jarvik 1948, fig. 36A; Jessen 1966, fig. 1A–B), *Powichthys* (Jessen 1975: figs. 1A–C, E; 2); Text-fig. 9.

  (c) The FP of the prefrontal lies in the same position as the pore-group in the posterior tectal (Text-figs 2D, 9; Gross 1956, fig. 1A; Jarvik 1948, fig. 38K; Jessen 1966, fig. 4B). The position of these groups of foramina supports the view that the posterior tectal is homologous with at least the upper part of the prefrontal of *Discosauriscus* (Klembara, in press b).

  (d) The FP of the left frontal is situated in exactly the same place as the pore-group of some osteolepids, i.e. in the corner formed by the supraorbital sensory canal laterally and the anterolateral portion of the frontal pit-line medially (Text-figs 2B, 9; Jarvik 1948, fig. 79F). Such a position of the frontal FP provides further evidence that the frontal bone of *Discosauriscus* is homologous with the bone called frontal in the 'orthodox' or 'traditional' terminology in osteolepiforms (Klembara 1992, in press b); it supports the view that the frontals in *Discosauriscus* are homologous with the bones enclosing the pineal foramen in osteolepiforms (Text-fig. 9).

  (e) The position of the FP in the postfrontal corresponds very well to the position of the pore-group in the dermosphenotic (Text-figs 2C, 9; Jarvik 1948, pl. 22, fig. 3; Jessen 1966, fig. 1A–B). As for the different position of the junction of infraorbital and supraorbital sensory canals in osteolepiforms and *Discosauriscus* see Klembara (in press a).

  (f) The FP in the intertemporal of *Discosauriscus* lies in the sensory groove or close to the intertemporal pit-line. The same situation occurs in rhipidistians, although the pore-group of the intertemporal lies in the region of different section of sensory canal system (Text-figs 2F, 9; Gross 1956, figs 2B, G; Jessen 1966, figs 4A, C; Bjerring 1972, figs 1A, 2, 3, 4C, 6).

  (g) The position of the FPs in the lacrimals of D54, D81 and K195 (Text-figs 8C, 9) corresponds to the position of the lacrimal pore-group in osteolepids (Jarvik 1948, figs 22E–F, 36A, 39E, G, 67A; Jessen 1966, fig. 1A; Text-fig. 9).

  (h) The maxillary FPs lie in the anterior portion of the bone (Text-fig. 8A–B), in exactly the same place as the pore-group in the osteolepid *Latvius* (Jessen 1966, fig. 1A; Text-fig. 9).

  (i) The FPs in the jugals lie in close vicinity to the junction of the infraorbital and jugal sensory grooves (Text-fig. 8G, I) which is identical in position to those of the pore-groups of jugals in osteolepids (Jarvik 1948, figs 22E, 36A, 67A; Jessen 1966, fig. 1A; Text-fig. 9).

  (j) The FPs of the squamosal lie in the posterior section of the jugal sensory groove on the ornamented surface of the squamosal, i.e. in the posterior part of the anterior half of the squamosal length (Text-fig. 8F, H). This corresponds to the position of squamosal pore-groups found in osteolepids (Jarvik 1948, figs 22F, 36A, 73A; Jessen 1966, fig. 1A), although the squamosal (or temporal) embayment is absent in the latter (Text-fig. 9).

  (k) The position of FPs in the dentaries (Text-fig. 8D–E) is comparable to the pore-groups of the anterior regions of the lower jaws of osteolepids (Jarvik 1948, figs 36A, 59F; Text-fig. 9).

From the above results, it can be seen that the only distinct morphological difference between the pore-group of rhipidistians and the FP of *Discosauriscus*, is that in the latter the group of foramina lies in a more distinctly developed pit and that, inside this pit, these foramina lie in still smaller pit structures. Unlike the pore-groups, the FPs occur also in parietals, supratemporals, tabulars and postparietals. Many striking similarities indicate, however, that the FPs and the pore-groups could be homologous structures and that they housed functionally identical organs.

The cranial pits of arthrodires

The groups of pits in the ornamented surface of some cranial bones of relatively small individuals of the arthrodire *Ctenurella*, were preliminarily described by Ørvig (1971, p. 30, fig. 6A). They are distinct, rounded pits arranged in a more or less pronounced reticular pattern. At the bottom of each pit, the foramen or foramina are observable. According to Ørvig (1971, p. 31) '...the 'pitted' areas seem to bear definite relations to the lateral line canals'.

In *Ctenurella*, as in *Discosauriscus*, the foramen or the groups of foramina are situated in distinct, rounded pits which lie close to the lateral line canals (Ørvig 1971, fig. 6A; Text-fig. 9). Although Ørvig did not give much information about the size, the morphology of the inner surface of the pit, or the number of foramina in the bottom of the pits, it seems that the whole morphology and the position of these pits in *Ctenurella* and the FPs of *Discosauriscus* are very similar. This suggests that the structures in the two animals may have had the same function.

INTERPRETATION AND CONCLUSIONS

On the basis of the position of the pore-groups, Jarvik (1948) and Bjerring (1972) deduced that the pore-group canals probably carried small peripheral nerves of the lateralis system. Jarvik (1948, p. 137) proposed, therefore, that the groups of pores 'mark the position of groups of some cutaneous sensory organs of somewhat the same type as the ampullae of Lorenzini in Elasmobranchs, the nerve-sacs of Teleostomian fishes...and 'die Flaschenförmige Organe' of Dipnoi...' (Jarvik 1980, p. 205). Bjerring (1972) suggested that the peripheral nerves of the lateralis system might have supplied a specific epidermal sensory area which perhaps was responsible for the reception of thermal stimuli (however, according to Bjerring 1986, the pore-groups are evidence for electroreception in osteolepids).

Ørvig (1971, p. 31) regarded the groups of pits in some dermal cranial bones in *Ctenurella*, 'as the sites of comparatively large groups of cutaneous sense organs resembling, or closely related to, ampullae of Lorenzini'. According to Ørvig (1971), the individual pits originally could have housed the ampullae of Lorenzini or clusters of these (similar to those in extant selachians and holocephalians).

As well as fishes, ampullary organs have also been found in representatives of two groups of extant tetrapods: the caecilian *Ichthyophis* (Hetherington and Wake 1979) and the urodeles *Triturus*, *Salamandra* and *Ambystoma* (Fritzsch and Wahnschaffe 1983; Northcutt 1989). However, as in extant fishes, the ampullary organs of urodeles do not leave traces in the external surface of the dermal cranial bones. As was shown by Fritzsch and Wahnschaffe (1983), the ampullary organ, unlike the neuromast organ, is more or less recessed below the epidermis (usually below the basement membrane) and connected to the surface by a canal (Fritzsch and Wahnschaffe 1983, p. 491, figs 6–7, 10, 20). This canal may be relatively long and is delineated by epidermal cells. The diameter of the ampullary organs ranges from 60–80 μm. The ampullary organs form groups of two to five organs (never linearly arranged) and sometimes three to five organs are found at the base of one canal (Fritzsch and Wahnschaffe 1983, fig. 8). They accompany the rows of neuromast organs. Unlike the neuromast organs, only one afferent fibre innervates each ampullary organ or groups of organs. During the terrestrial phases of the urodele's life, the canal of the ampullary organ is closed by the outer epidermal layer.

From the comparisons of the ampullary organs of urodeles and FPs of *Discosauriscus*, it is here concluded that the FPs probably housed groups of ampullary organs as found in urodeles and caecilians. This conclusion is supported by morphological and positional similarities of the compared structures. The structure of the inner surface of the FPs is entirely consistent with the possibility of housing such groups of ampullary organs. The inner surface of the FP is smooth or more or less irregular consisting of various pits, depressions, short grooves or canals, each having one small foramen at the base. These structures probably housed the groups of ampullary organs supplied by peripheral nerves of the lateralis system. The size of a group of ampullary organs corresponds very well to the size of one pit structure in the inner surface of the FP. If this interpretation of the *Discosauriscus* FPs is correct, the osteolepiform pore-groups also mark the possible presence of ampullary organs.

The ampullary organs within the head of *Salamandra* occur mostly around the external nares and eyes, although in *Ambystoma mexicanum* they occur also at the base of the gills (Fritzsch and Wahnschaffe 1983). In *Ichthyophis*, however, they are also present in the posterodorsal region of the head (Hetherington and Wake 1979), as in *Discosauriscus*. The distribution of the ampullary organs within the head in urodeles differs from the condition in *Discosauriscus* where the FPs are not so abundant and occur mostly in the posterior part of the skull table. In osteolepiforms, the individual pore-groups are also less abundant (as in *Discosauriscus*), but occur, as in urodeles and *Ichthyophis*, mostly in the frontoethmoidal region of the skull. However, the position of most of the pore-groups in the individual skull roof bones of osteolepiforms and of the FPs in *Discosauriscus* is conspicuous (see above and Text-fig. 9) and, together with the morphological similarities, indicate the homology of both structures as well as of the bones which bear them. This is in agreement with the conclusions based mostly on the morphology and position of pit-lines in the dermal skull roof bones in *Discosauriscus* that the 'orthodox' terminology of the skull roof bones used in osteolepiforms (and related fish groups) is correct (Klembara 1992, in press b; Text-fig. 9). It implies that the bones enclosing the pineal (and/or parapineal) foramen are the frontals. The distribution of FPs and pore-groups in skull roofs of *Discosauriscus* and rhipidistians (especially osteolepids but also *Powichthys* and *Youngolepis*) clearly indicates their evolutionary relationship.

It has been shown that, in Recent urodeles, the lateral line system consists of two types of receptors with two different properties: mechanoreceptive neuromasts and electroreceptive ampullary organs (e.g. Fritzsch 1981*a*, 1981*b*; Münz *et al.* 1982, 1984; Bullock 1982; Himstedt *et al.* 1982; Fritzsch and Wahnschaffe 1983). Münz *et al.* (1982) showed that the axolotl (*Ambystoma mexicanum*) was able to detect weak electrical fields. Himstedt *et al.* (1982) observed in the axolotl, changes in prey capture behaviour during electrical stimulation (however, this phenomenon appeared only after visual and mechanical stimuli). They concluded 'that the electrosensory system may help to localize prey objects which produce electrical fields...'. According to Münz *et al.* (1984, p. 42), 'the feeding behavior may normally be guided not by the electroreceptive system alone, but rather by cooperation of the electroreceptive, mechanoreceptive, and olfactory systems'. The possession of electrical fields in insect larvae, snails, tadpoles and fish was recorded by Peters and Bretschneider (1972). If the FPs in *Discosauriscus* housed ampullary organs, this implies that this Early Permian tetrapod was electroreceptive and used this ability in a similar way to Recent urodeles. Likewise, the same is true for rhipidistians. The presence of the FPs in *Discosauriscus* also supports the recognition of this tetrapod (in the size category considered here) to be larval (Klembara 1993, 1994, in press a, b). The possible existence of the electroreceptive ampullary organs in *Discosauriscus* supports the view of Bullock, Northcutt and Bodznick (1982) that electrosensitivity is phylogenetically as old as the major vertebrate sensory systems.

Acknowledgements. For information on the structure of pore-groups and pits of various fossil fishes, I would like to thank Drs H. C. Bjerring and T. Ørvig (Swedish Museum of Natural History, Stockholm). I am indebted to Dr A. R. Milner (Birkbeck College, London) for reading the manuscript and linguistic correction of the text. I thank Mrs Z. Šulavíková (Faculty of Natural Sciences, Bratislava) for making the photographs and typing the manuscript. For the scanning electron micrograph (Text-fig. 3D), I thank Dr J. Krištín (Faculty of Natural Sciences, Bratislava). Two illustrations (Text-figs 1B and 5B) were made by Juraj Gullár (Bratislava). This project was partly supported by SLOVNAFT a.s. SAS 31322B32, G7 to JG.

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ABBREVIATIONS

AN	angular	PA	parietal	TA	tabular
DE	dentary	PFR	prefrontal	TA.pl	tabular pit-line
DSO	dermosphenotic	PMX	premaxillary	TA-PP	tabulo-postparietal
ET	extratemporal	PO	postorbital	ant.PA.pl	anterior parietal pit-line
ESC.l	lateral extrascapular	POFR	postfrontal		
ESC.l.pl	lateral extrascapular pit-line	POP	preopercular	ethm.comm	ethmoidal commissure
ESC.m	median extrascapular	PP	postparietal	for.p	foraminate pit
FR	frontal	PP.pl	postparietal pit-line	ior.s.gr	infraorbital sensory groove
FR.pl	frontal pit-line	PSP	postsplenial	ju.s.gr	jugal sensory groove
IT	intertemporal	QJ	quadratojugal	long.PA.pl	longitudinal parietal pit-line
IT.pl	intertemporal pit-line	SAN	surangular	m.s.gr	main sensory groove
JU	jugal	SMX	septomaxillary	man.s.gr	mandibular sensory groove
LA	lacrimal	SOP	subopercular	post.obl.PA.pl	posterior oblique parietal pit-line
Lj	lower jaw	SP	splenial	pot.s.gr	postotic sensory groove
MX	maxillary	SQ	squamosal	sor.s.gr	supraorbital sensory groove
NA	nasal	ST	supratemporal	st.comm.s.gr	supratemporal commissural sensory groove
OP	opercular	ST.pl	supratemporal pit-line	tr.PA.pl	transverse parietal pit-line

LATE ORDOVICIAN LINGULATE BRACHIOPODS FROM ESTONIA

by LEONID POPOV, JAAK NÕLVAK *and* LARS E. HOLMER

ABSTRACT. The lingulate brachiopod fauna from the Upper Ordovician Harju Series of southern Estonia consists of nine taxa, including the new acrotretid species *Rhinotreta laeta*, *Opsiconidion praecursor*, and *Scaphelasma scutula*. The unusual brachiopod-dominated assemblage was isolated by acid etching, mainly from a thin aphanitic limestone unit in the lower Pirgu Stage of the Viljandi core. The pitted micro-ornament on the larval and postlarval shell and the deep emarginature (pedicle notch) of the lingulide *Rowellella minuta* suggests that it belongs to the Zhanatellidae.

LINGULATE brachiopods, mainly lingulides and acrotretides, are known to be abundant in the early and middle Ordovician sequences of Baltoscandia (Gorjansky 1969; Biernat 1973; Holmer 1986, 1989), but less is known about the late Ordovician (Harju Series) faunas (e.g. Bergström 1968; Holmer 1986; Popov and Nõlvak 1987). The object of this paper is to describe a diverse assemblage of 'micro-brachiopods' (in the sense of Wright and McClean 1991) from the Upper Ordovician Nabala to Pirgu stages (lower–middle Ashgill; upper Pusgillian–lower Cautleyan) of southern Estonia. The described fauna is compared with other late Ordovician lingulate assemblages from Ireland and Sweden.

GEOLOGICAL SETTING, STRATIGRAPHY AND CORRELATION

Most of the lingulate assemblage described here comes from the Nabala–Vormsi interval in the Viljandi core, southern Estonia, but a few specimens originate from the same interval in the Eikla core on the island of Saaremaa (Text-fig. 1); the Upper Ordovician (Harju Series) succession in the latter core has been discussed by Nõlvak (1986), and Nõlvak and Grahn (in press). According to Põlma (1973, fig. 1), the Viljandi core is situated just at the southern boundary of the transitional zone between the Central Baltoscandian and North Estonian confacies belts, whilst the Eikla core is within the North Estonian confacies belt (see also Jaanusson 1976, text-fig. 7).

The upper Ordovician chitinozoan biostratigraphy of the Viljandi core was discussed by Nõlvak (1986), but the lithostratigraphical succession in the core has not been published. The lower part of the Nabala Stage is represented by the Mõntu Formation, consisting mainly of argillaceous limestone with some minor amounts of glauconite. Lingulates are rare, with only a few valves of *Rhinotreta laeta* sp. nov. and *Spondylotreta* cf. *parva* known; both these forms range almost throughout the entire sequence (Text-fig. 2). Above the Mõntu Formation lies a 0·4 m interval of aphanitic limestone (that is, a dense, high-carbonate calcilutite with a conchoidal fracture) belonging to the Saunja Formation; the lower and upper boundaries are marked by hardgrounds. In the unit, lingulates are extremely rare. The Tudulinna Formation of the Vormsi Stage, 6·3 m thick, is represented by spotted red argillaceous marlstones, with some beds of argillaceous and nodular argillaceous limestone; this part of the sequence has generally rare lingulates, but there is an increase in diversity and abundance towards the top, where the majority of the recorded species appear, including *Acanthambonia portranensis*, *Scaphelasma scutula* sp. nov. and *Eoconulus semiregularis*.

[Palaeontology, Vol. 37, Part 3, 1994, pp. 627–650, 7 pls]

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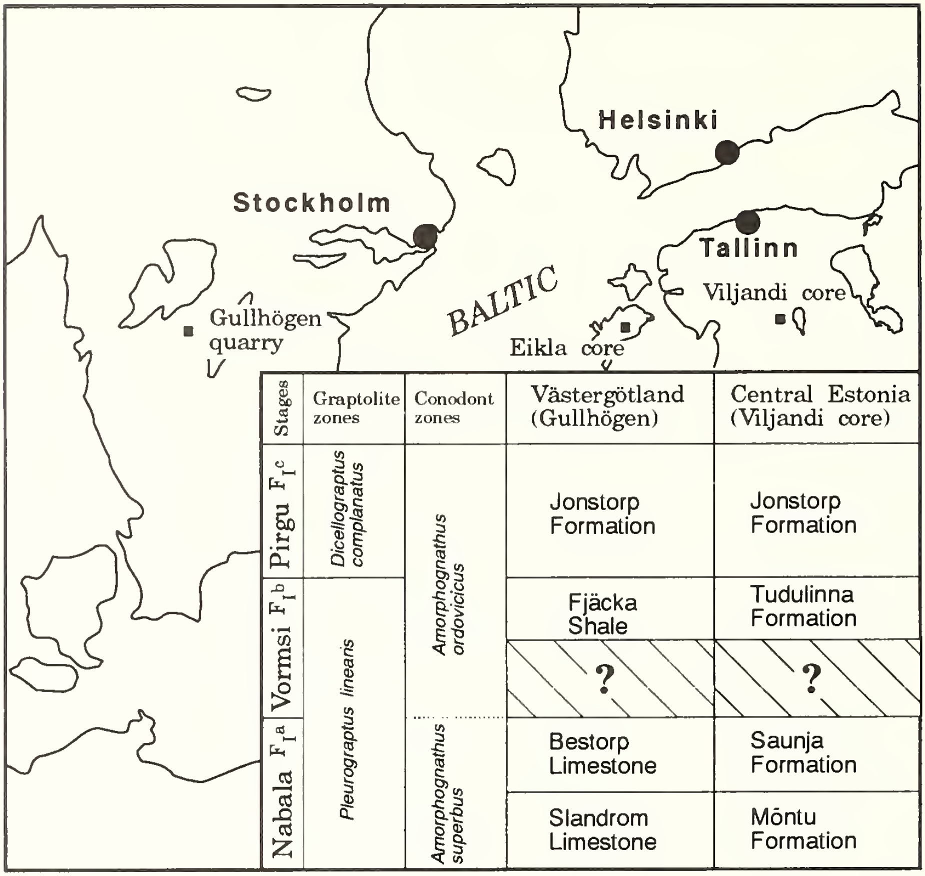


Stages	Graptolite zones	Conodont zones	Västergötland (Gullhögen)	Central Estonia (Viljandi core)
Pirgu F_I^c	*Dicellograptus complanatus*	*Amorphognathus ordovicicus*	Jonstorp Formation	Jonstorp Formation
Vormsi F_I^b	*Pleurograptus linearis*		Fjäcka Shale	Tudulinna Formation
			?	?
Nabala F_I^a		*Amorphognathus superbus*	Bestorp Limestone	Saunja Formation
			Slandrom Limestone	Mõntu Formation

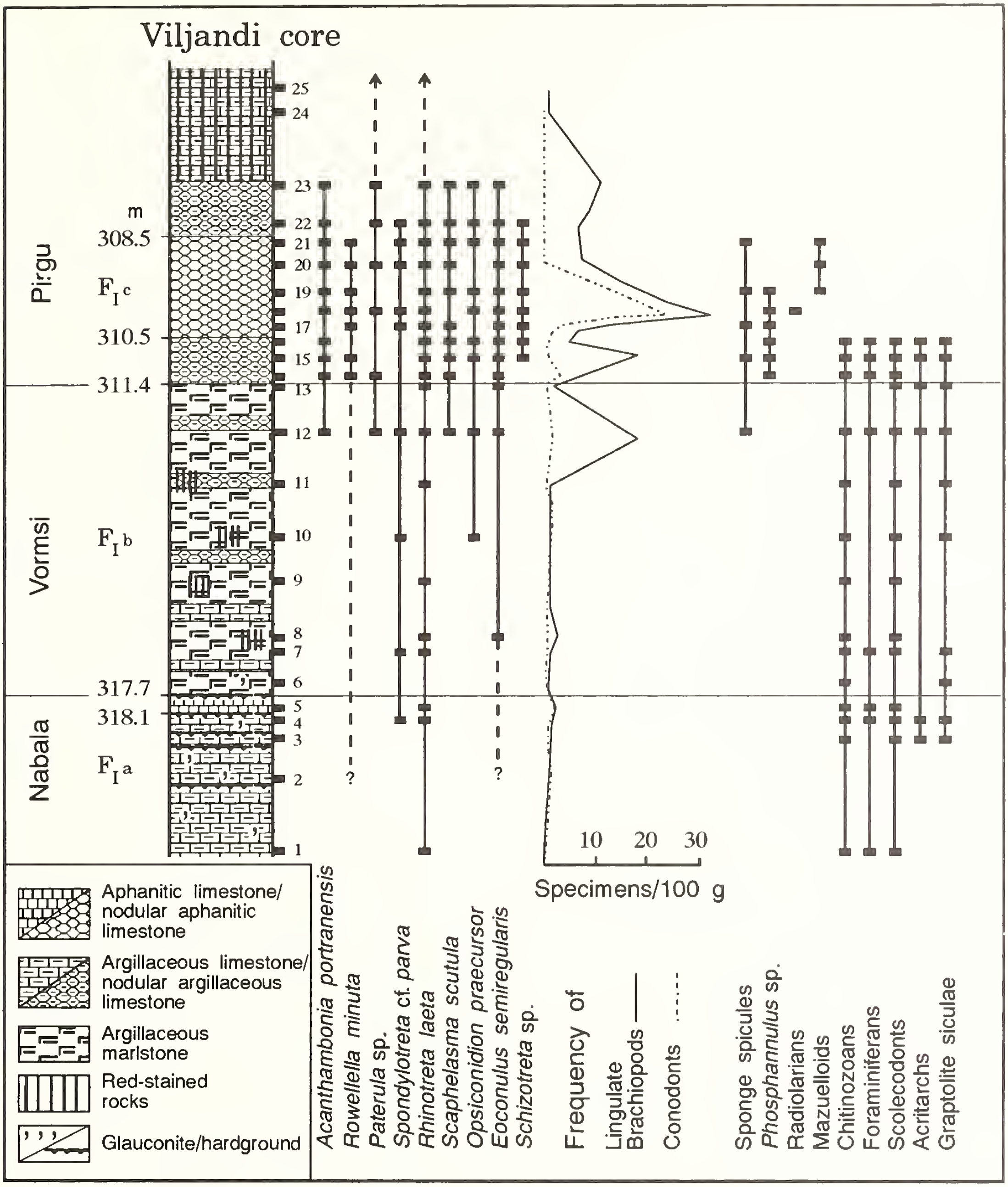
TEXT-FIG. 1. Map of Baltoscandia showing the location of Viljandi and Eikla cores, Estonia, and Gullhögen quarry, Sweden; stratigraphical scheme after Nõlvak and Grahn (in press).

The major portion of the described fauna was isolated from the lower Pirgu Stage, within which an almost three metre thick interval (308·5–331·4 m) of nodular argillaceous limestone and light coloured, nodular aphanitic limestone yielded over thirty lingulate specimens per 100 g. The aphanitic interval is overlain by red argillaceous nodular limestones of the Jonstorp Formation.

Of the recorded lingulates, only *Acanthambonia portranensis* Wright, 1963 is not described below as the material of this species from the Vorsmi–Pirgu stages in the Viljandi core (Text-fig. 2) was described in detail by Popov and Nõlvak (1987). Gorjansky (1969, p. 49) described this species from the Pirgu Stage of southern Estonia.

The distribution of the associated fauna, including mazuelloids, radiolarians, conodonts, and sponge spicules is recorded in Text-figure 2, but is not discussed in detail here. However, it is of note that rich lingulate assemblages are commonly associated with sponge spicules (Text-fig. 2; see also Holmer 1986, 1987); possible sponge-lingulate associations have been described from the Cambrian by Whittington (*in* Conway Morris *et al.* 1982, p. 25, pl. R) and by Lenz (1993) from the Silurian of Canada, where numerous specimens of the lingulide *Paterula* (referred to as *Craniops* sp. by Lenz) are apparently attached around the oscular margin of sponges.

At the generic level, the Estonian lingulate assemblage has a composition similar to that of the Slandrom and Bestorp limestones at Gullhögen quarry, Västergötland (Text-fig. 1) described by



TEXT-FIG. 2. Stratigraphical column of the Nabala–lower Pirgu interval in the Viljandi core, showing the range of lingulates, frequency of lingulates and conodonts, and the range of associated groups of microfossils.

Holmer (1986); *Rowellella*, *Paterula*, *Rhinotreta*, *Scaphelasma*, *Eoconulus*, *Acanthambonia* and *Schizotreta* are present in the somewhat older Swedish fauna, which also contains numerous mazuelloids, radiolarians, sponge spicules and the problematic *Phosphannulus* (Holmer 1987). At the specific level, however, the Estonian and Västergötland assemblages are distinct. *Opsiconidion* *praecursor* sp. nov. is the oldest known species of the genus and the most distinctive element of the Estonian assemblage; the genus is not known from the late Ordovician of Sweden.

The Estonian lingulate assemblage is also markedly similar to the assemblage described by Wright (1963) from the Portrane Limestone (Ashgill, Cautleyan) of Ireland, which includes *Rowellella minuta*, *Paterula* cf. *perfecta*, *Spondylotreta* cf. *parva*, *Eoconulus transversus*, *Schizotreta concava*, and *Acanthambonia portranensis*.

McClean (1988, 1989) and Wright and McClean (1991) described a diverse micro-brachiopod fauna from the Chair of Kildare Limestone (Ashgill, Rawtheyan), eastern Ireland, that includes *Acanthambonia portranensis*, although a formal description of this fauna has not been published (McClean 1988). As noted by Wright and McClean (1991), it has been assumed that there was a general decline in the number of lingulate species towards the end of the Ordovician (e.g. Cocks 1979), but the new Estonian and Irish assemblages indicate that this group remained diverse and abundant in beds of Ashgill age.

SYSTEMATIC PALAEONTOLOGY

The classification and terminology of lingulate brachiopods used here mainly follows that of Rowell (1965), Koneva (1986) and Holmer (1989). Measurements (in millimetres) were made with a binocular microscope at × 56 magnification. The method described by Krause and Rowell (1975) is followed in the presentation of the biometric data; vectors of means and variance-covariance matrices were calculated for each set of measurements (Tables 1–6; Text-figs 3–6). The mean, standard deviation (s), and number (N) of measured specimens are given.

All figured specimens are housed in the Institute of Geology, Estonian Academy of Sciences, Tallinn.

Class LINGULATA Gorjansky and Popov, 1985
Order LINGULIDA Waagen, 1885
Family ZHANATELLIDAE Koneva, 1986

Diagnosis. Shell subcircular to elongately suboval in outline; larval and postlarval shell with finely pitted micro-ornament. Ventral valve with flattened pseudointerarea, bisected by deep pedicle groove; flexure lines variably developed; beak with semicircular emarginature (pedicle notch). Dorsal pseudointerarea divided by median groove or undivided; umbonal muscle paired; mantle canals baculate in both valves, with submarginally placed *vascula lateralia* and well developed dorsal *vascula media*.

Genera included. Zhanatella Koneva, 1986; *Fossuliella* Popov and Ushatinskaya, 1992; ?*Kyrshbaktella* Koneva, 1986; *Rowellella* Wright, 1963.

Discussion. According to Koneva (1986), the zhanatellids are distinguished mainly by having a deep, semicircular pedicle notch, which was termed the 'emarginature'. Our unpublished studies into the

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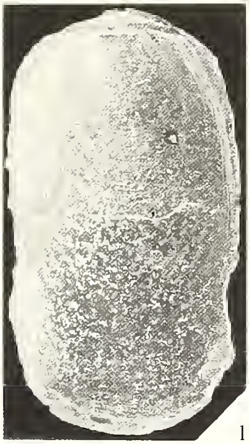
EXPLANATION OF PLATE 1

Figs 1–4. *Rowellella minuta* Wright, 1963; lower Pirgu Stage. 1, Br 1623, (depth 309·1 m); ventral interior; × 50. 2, Br 1624, (depth 310·9 m); dorsal exterior; × 50. 3, detail of the larval portion of shell shown in fig. 2; × 200. 4, detail of pitted micro-ornament of shell in 2; × 940.

Figs 5–7. *Spondylotreta* cf. *parva* Wright, 1963; lower Pirgu Stage. 5, Br 1627 (depth 310·1 m); juvenile dorsal interior; × 100. 6, Br 1628 (depth 310·3 m); ventral larval shell; × 150. 7, Br 1626 (depth 309·1 m); dorsal exterior; × 75.

Figs 8–9. *Schizotreta* sp.; lower Pirgu Stage. 8, Br 1632 (depth 308·7 m); dorsal exterior; × 50. 7, Br 1631 (depth 310·9 m); dorsal exterior; × 50.

All scanning electron micrographs of specimens from the Upper Ordovician of the Viljandi core, Estonia.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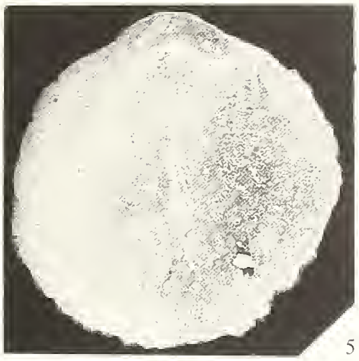
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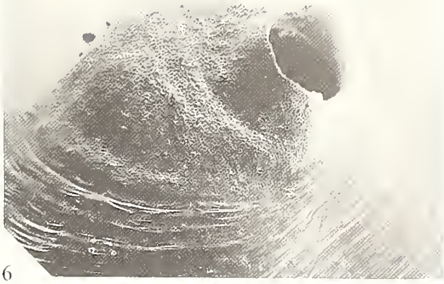
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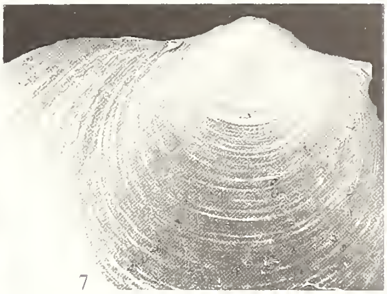
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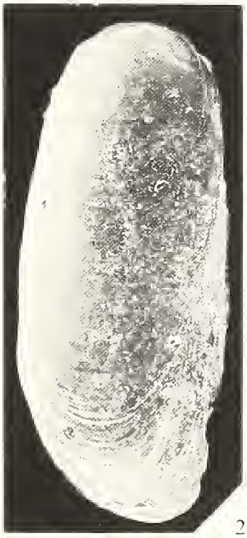
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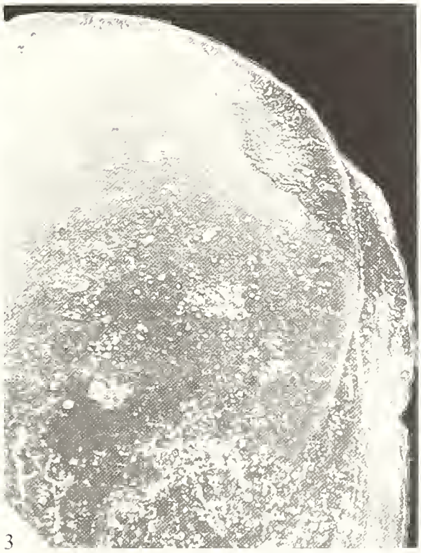
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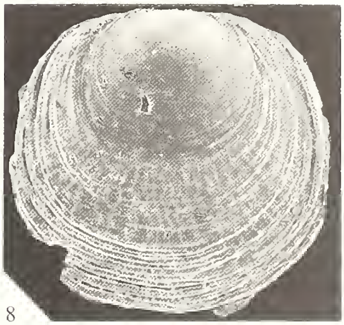
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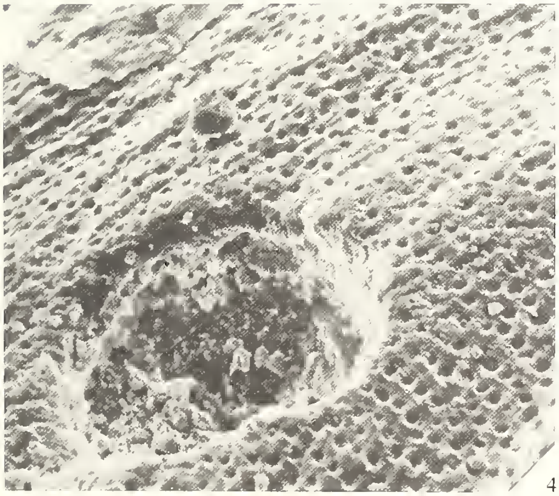
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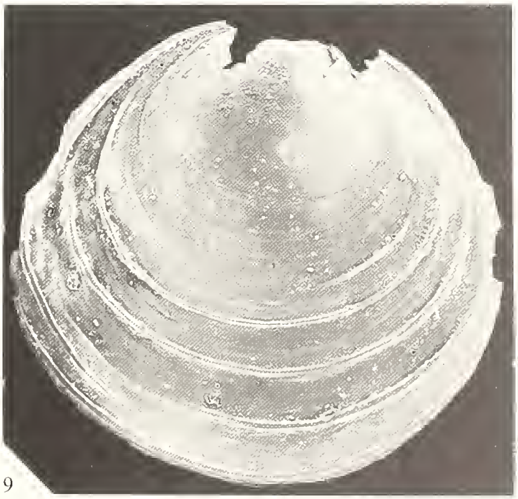
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POPOV *et al.*, *Rowellella*, *Spondylotreta*, *Schizotreta* morphology of *Zhanatella* suggest that a pitted larval and postlarval shell also is a diagnostic character of the family. Both of these features are present in *Rowellella*, which is here referred to the zhanatellids. Koneva (1986) also suggested that *Kyrshabaktella* is a zhanatellid, but this is more problematic, since it is characterized by a smooth larval and postlarval shell.

Genus ROWELLELLA Wright, 1963

Type species. By original designation; *Rowellella minuta* Wright, 1963, from the Ashgill of Ireland.

Rowellella minuta Wright, 1963
Plate 1, figures 1–4

1963 *Rowellella minuta* sp. nov. Wright, p. 233, pl. 1, figs 8–12, 14–18.

Holotype. BB28223 (complete shell; in the Natural History Museum, London) from the Portrane Limestone (Ashgill, Cautleyan), Portrane, Co. Dublin, Ireland.

Estonian material. Seven ventral and five dorsal valves; figured: Br 1623, 1624.

Diagnosis. Shell dorsi-biconvex, elongately subtriangular in outline with close to parallel lateral margins; ornamentation of well developed concentric lamellae; larval and postlarval shell finely pitted.

Discussion. The Estonian specimens are more or less identical to the Irish material in outline and ornamentation. However, the pitted micro-ornamentation has not previously been described from the type material. The semielliptical larval shell is about 0·2 mm wide and lacks growth lines (Pl. 1, fig. 3); it is ornamented by shallow and circular pits about 1·6–2·4 μm in diameter (Pl. 1, fig. 4). The postlarval shell has a similar type of micro-ornamentation with subcircular and transversely oval pits, 1·2–3·9 μm across. A similar type of pitting was described by Holmer (1986, 1989) from several species of *Rowellella*.

Family PATERULIDAE Cooper, 1956

Diagnosis. Shell dorsi-biconvex, inequivalved. Both valves with holoperipheral growth and lacking pseudointerareas; larval and postlarval shell finely pitted; visceral fields of both valves large, extended anterior to mid-valve; *vascular lateralia* of both valves submarginal, arcuate. Ventral valve with emarginature (pedicle notch).

Genera included. *Paterula* Barrande, 1879.

Discussion. *Elliptoglossa* Cooper and *Lingulops* Hall were previously included within the family; but they differ from paterulids in having a smooth larval and postlarval shell, marginal beaks in both valves, rudimentary pseudointerareas, and no pedicle notch. This suggests to us that *Elliptoglossa* and *Lingulops* are more closely related to the Obolidae. The Zhanatellidae is the only other lingulide stock that is characterized by having a deep pedicle notch (emarginature) and a pitted larval and postlarval shell.

Genus PATERULA Barrande, 1879

Type species. By original designation; *Paterula bohemica* Barrande, 1879, from the Caradoc of Bohemia.

Paterula sp.

Plate 2, figures 1–6

?1963 *Paterula* cf. *perfecta* Cooper; Wright, p. 235, pl. 2, figs 3–5, 8–10, 13, 16.

Material. Three ventral and twelve dorsal valves; Br 1620–1622 are figured.

Remarks. Paterula is a taxonomically complicated genus; without detailed knowledge concerning the micro-ornamentation and internal features, most species seem to be indistinguishable.

The valves examined are similar to the specimens described by Wright (1963) as *Paterula* cf. *perfecta* from the Portrane Limestone, but we have too few specimens to make a detailed comparison. The Estonian specimens are also somewhat similar to *Paterula* cf. *bohemica* figured by Henningsmoen (1948) from the Fjäcka Shale of the Kullatorp core, Kinnekulle, Sweden.

The subcircular larval shell of *Paterula* sp. is about 50–60 μm in diameter; it is covered by flat-bottomed, rounded to polygonal pits, each 2·4–3·6 μm across (Pl. 2, fig. 4). The pits are separated from one another by elevated ridges, but sometimes they show a cross-cutting relationship, similar to that found on the larval shell of the acrotretoid *Opsiconidion* (Bitter and Ludvigsen 1979). The outer boundary of the larval shell is poorly defined, and there is a gradual change to the net-like pattern of rhombic pits, each about 5·8 μm across, that covers the rest of the postlarval shell (Pl. 2, figs 4–5). An identical type of pitted micro-ornament was described by Holmer (1986) on *Paterula* spp. from the Slandrom Limestone of Sweden.

Order ACROTRETIDA Kuhn, 1949
Family ACROTRETIDAE Schuchert, 1893
Genus SPONDYLOTRETA Cooper, 1956

Type species. By original designation; *Spondylotreta concentrica* Cooper, 1956, from the middle Ordovician of Alabama.

Diagnosis. Ventral valve high to low conical; ventral pseudointerarea well defined, catacline or slightly procline, with distinct interridge; pedicle foramen forming short tube within larval shell; ventral interior with pedicle tube along posterior slope, continued as forked ridge, supported apically by median septum. Dorsal valve slightly convex; dorsal pseudointerarea wide, divided by median groove; dorsal interior with long and high, triangular median septum, and median buttress.

Discussion. Spondylotreta is most similar to *Acrotreta* Kutorga; the type species of the latter, *A. subconica* Kutorga was revised by Holmer and Popov (1994). Amongst other characters, *Acrotreta* differs from *Spondylotreta* in having a higher conical ventral valve, with a pedicle foramen that is not completely enclosed within the larval shell. *Acrotreta* appears to have its main range in the lower and middle Ordovician, whilst *Spondylotreta* is known primarily from the middle to upper Ordovician.

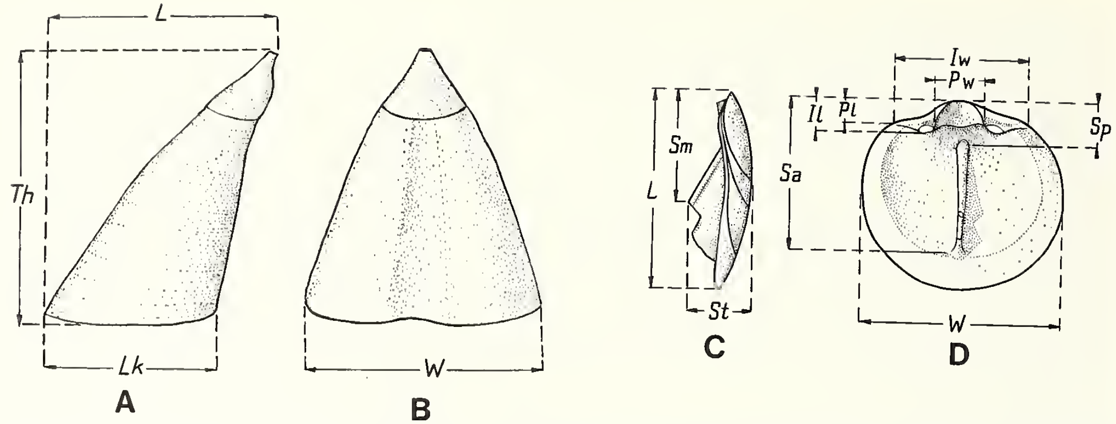
Spondylotreta cf. *parva* Wright, 1963

Plate 1, figures 5–7

cf. 1963 *Spondylotreta parva* sp. nov. Wright, p. 238, pl. 2, figs 17, 20–25; pl. 3, figs 1, 5, 9, 15.

Material. Five ventral and ten dorsal valves; Br 1626–1628 are figured.

Description. Shell transversely subcircular in outline. Ventral valve conical, with procline, slightly flattened pseudointerarea, bisected by distinct interridge. Pedicle foramen placed within the larval shell, and forming short external pedicle tube (Pl. 1, fig. 6). Ventral interior with internal pedicle tube, supported by apical process, forming high median septum; apical pits well developed, placed directly laterally to internal pedicle foramen.



TEXT-FIG. 3. *Opsiconidion praecursor* sp. nov. A–B, dorsal, and C–D, ventral valves, showing locations of measurements (Table 1). L, sagittal length; Lk, length of commissural plane; W, maximum width; Th, maximum depth of the valve; Il, length of dorsal pseudointerarea; Iw, width of dorsal pseudointerarea; Pw, width of median groove; Sp, point of origin of the median septum, measured from the sagittal posterior margin; Sm, point of maximum height of the median septum, measured from the sagittal posterior margin; Sa, length of median septum, measured from the sagittal posterior margin; St, height of median septum; Fa, distance from the anterior margin of the pedicle foramen to the sagittal posterior margin; Fp, distance from the posterior margin of the pedicle foramen to the sagittal posterior margin; A, distance from the sagittal posterior margin to the ventral apex.

Dorsal valve gently and evenly convex with shallow sulcus. Dorsal pseudointerarea orthocline with wide median groove. Dorsal interior with high triangular median septum buttressed posteriorly; dorsal cardinal muscle scars moderately large and transversely suboval in outline.

Shell is ornamented by fine, evenly spaced filae. Larval shell circular, about 130 μm in diameter (Pl. 1, fig. 7); larval ornamentation with large pits 2·4–4·0 μm in diameter, sometimes showing cross-cutting relationships, surrounded by clusters of small, irregularly distributed pits, 0·9–1·7 μm in diameter.

Discussion. There are virtually no differences between the Estonian specimens and those from Ireland. However, we do not have any well preserved adult valves and a closer comparison is not possible. Wright (1963) also described some large, poorly preserved fragments of *Spondylotreta* cf. *parva* that are equally difficult to compare closely with the Estonian form.

Family BIERNATIDAE Holmer, 1989

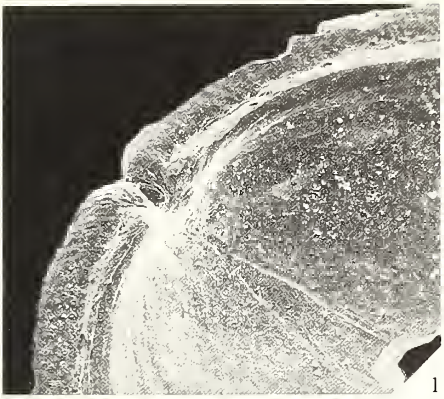
[*nom. trans.* Popov and Holmer, herein (*ex* Biernatinae Holmer, 1989, p. 131)]

EXPLANATION OF PLATE 2

Figs 1–6. *Paterula* sp. 1, Br 1620; Vormsi Stage; depth 312·5 m; ventral interior; × 75. 2, detail of emarginature of shell shown in fig. 1; × 150. 3, Br 1621; lower Pirgu Stage; depth 309·1 m; lateral view of dorsal exterior; × 50. 4, detail of apex of shell shown in fig. 3, showing pitted larval and postlarval shell; × 330. 5, detail of pitted postlarval portion of shell shown in fig. 3; × 1440. 6, Br 1622; lower Pirgu Stage; depth 311·3 m; ventral exterior; × 75.

Figs 7–8. *Opsiconidion praecursor* sp. nov.; Br 1646, holotype; lower Pirgu Stage; depth 310·1 m. 7, lateral view of dorsal interior; × 100. 8, plan view of dorsal interior; × 100.

All scanning electron micrographs of specimens from the Upper Ordovician of the Viljandi core, Estonia.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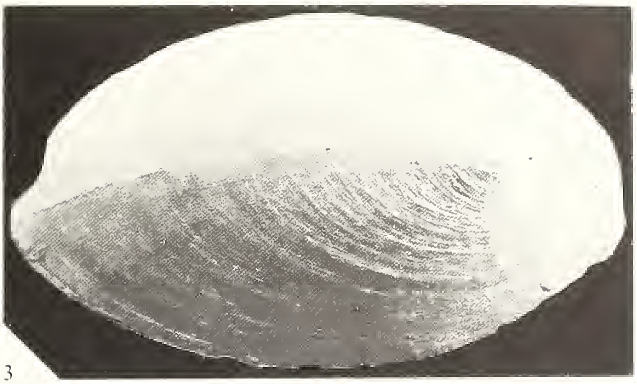
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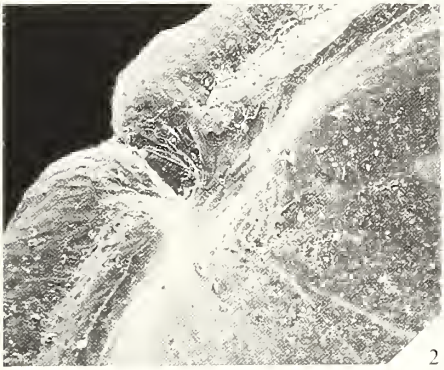
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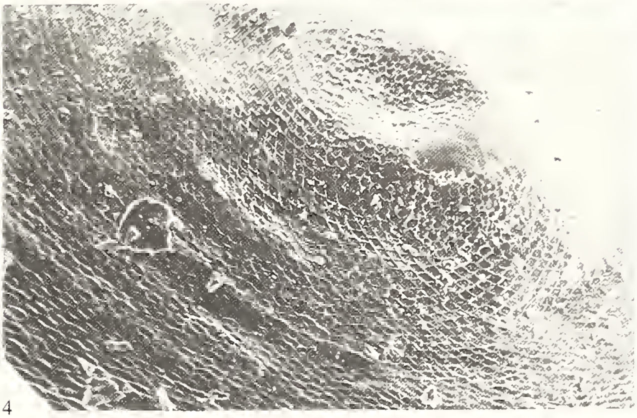
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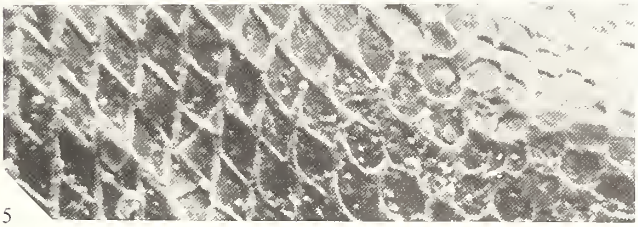
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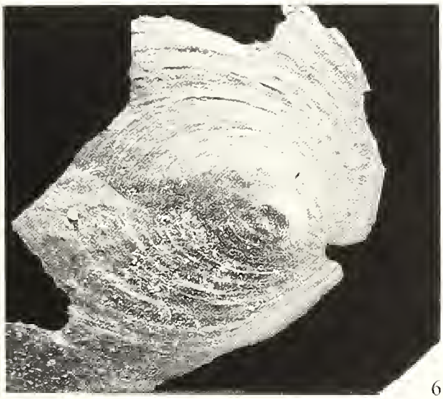
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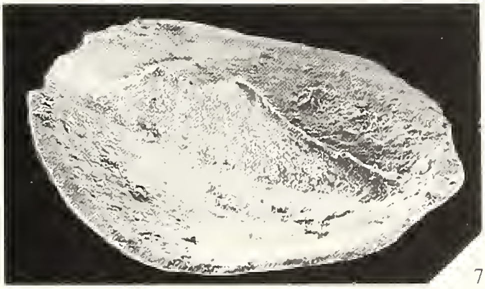
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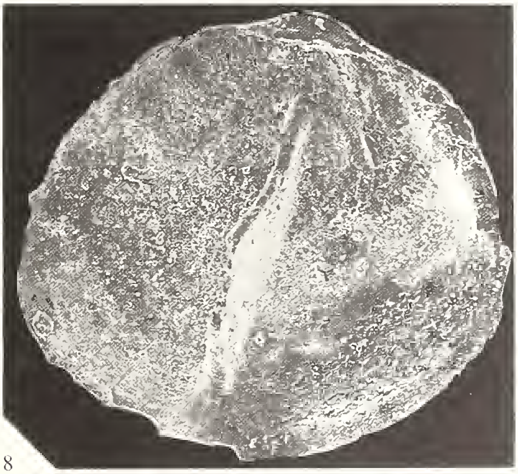
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POPOV *et al.*, *Paterula*, *Opsiconidion*

Diagnosis. Shell with narrow, curved posterior margin. Ventral valve strongly convex and apsacline. Ventral pseudointerarea poorly defined, usually lacking intertrough; apical process absent. Dorsal pseudointerarea small, with a tendency towards reduction; dorsal interior with median septum bearing convex surmounting plate or septal rod.

Genus OPSICONIDION Ludvigsen, 1974

Type species. By original designation, *Opsiconidion arcticon* Ludvigsen, 1974, from the Devonian of Yukon Territory.

Opsiconidion praecursor sp. nov.

Plate 2, figures 7–8; Plate 3; Text-figure 3

Derivation of name. Latin *praecursor* predecessor.

Type material. Holotype. Br 1646; dorsal valve from the lower part of Pirgu Stage, Viljandi core (depth 310·1 m), Estonia. Paratypes. Twenty seven ventral and twenty dorsal valves; Br 1644–1645, 1647–1649 are figured.

Diagnosis. Dorsal pseudointerarea reduced; dorsal median septum with single upper septal rod. Larval shell with pits of two sizes.

Description. Shell subcircular in outline, on average 91 per cent (s 3·4, N 10) as long as wide. Ventral valve highly conical, on average 110 per cent (s 13·5, N 5) as high as long. Ventral pseudointerarea apsacline, undivided or with poorly developed intertrough (Pl. 3, figs 1–3). Ventral interior without distinctive structures.

Dorsal valve gently convex and sulcate, with maximum height in the posterior one third of the valve length (Pl. 3, fig. 6). Dorsal pseudointerarea small, anacline, occupying on average 40 per cent (s 6·0, N 10) of valve width; median grove occupying on average 46 per cent (s 6·3, N 9) of the width of the pseudointerarea (Pl. 3, fig. 3). Dorsal interior with high, triangular median septum, originating on average 28 per cent (s 4·6, N 7) of the total length from the posterior margin, and extending for 85 per cent (s 4·1, N 10) of the length; single upper septal rod developed along the posterior slope of the septum; dorsal cardinal muscle scars poorly defined (Pl. 3, figs 4–5).

The larval shall is covered by pits of two sizes, with the larger ones, 2·9–4·9 μm in diameter, separated from one another by distinct elevated ridges, 0·7–2·1 μm in width, bearing clusters of extremely small pits (Pl. 3, fig. 7). The adult shell has a micro-ornamentation with concentric fila, forming radial rows of outwardly convex 'drapes' about 40 μm wide (Pl. 3, fig. 8).

Discussion. Opsiconidion praecursor sp. nov. is the oldest known species of the genus. It is very similar to *O. aldridgei* (Cocks 1979), from which it differs in having a proportionally smaller dorsal

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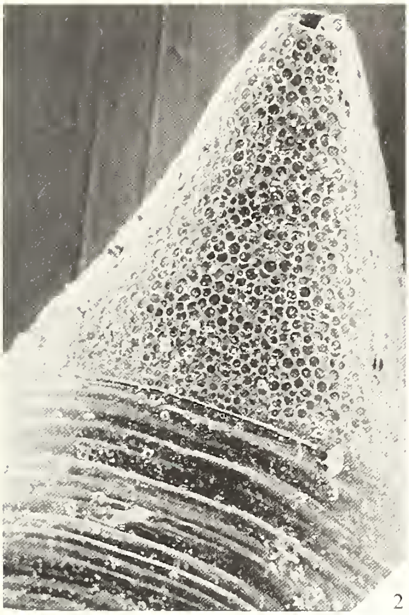
EXPLANATION OF PLATE 3

Figs 1–8. *Opsiconidion praecursor* sp. nov.; Viljandi core (1–7), Eikla core (8). 1, Br 1647; lower Pirgu Stage; depth 310·1 m; oblique posterior view of ventral exterior; × 100. 2, detail of shell shown in fig. 1, showing larval ornamentation; × 330. 3, Br 1644; Vormsi Stage; depth 312·5 m; posterior view of ventral exterior; × 100. 4, Br 1645; lower Pirgu Stage; depth 310·1 m; dorsal interior; × 100. 5, oblique lateral view of shell shown in fig. 4; × 200. 6, Br 1649; lower Pirgu Stage; depth 310·1 m; dorsal exterior; × 200. 7, detail of larval portion of shell shown in fig. 6; × 1120. 8, Br 1648; Nabala Stage; depth 284·7 m; detail of ornamentation of dorsal valve; × 720.

All scanning electron micrographs of specimens from the Upper Ordovician of Estonia.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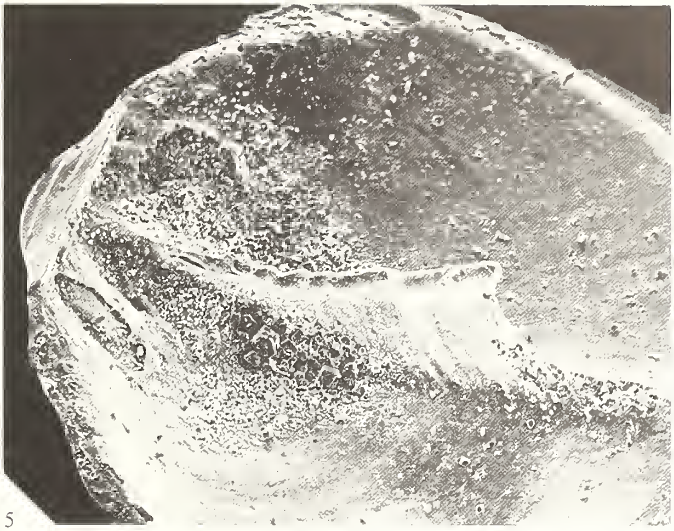
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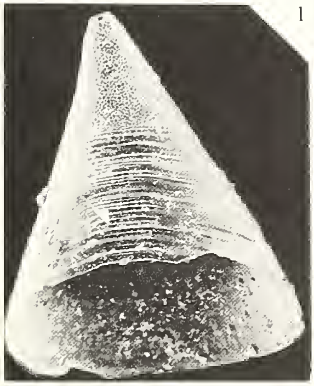
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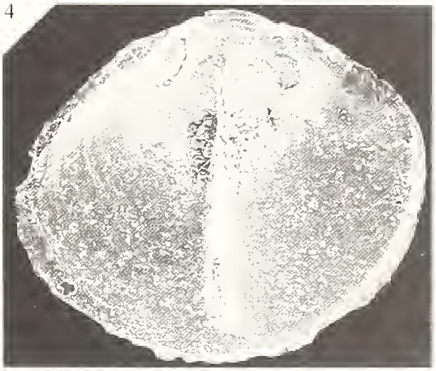
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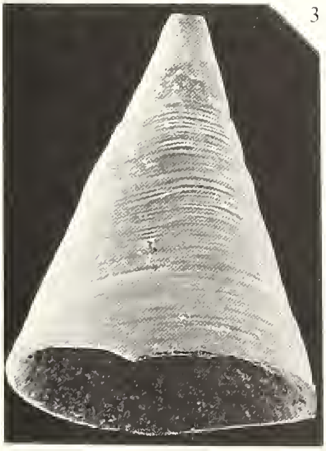
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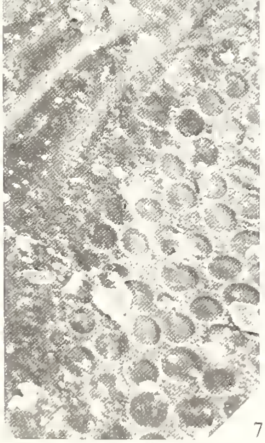
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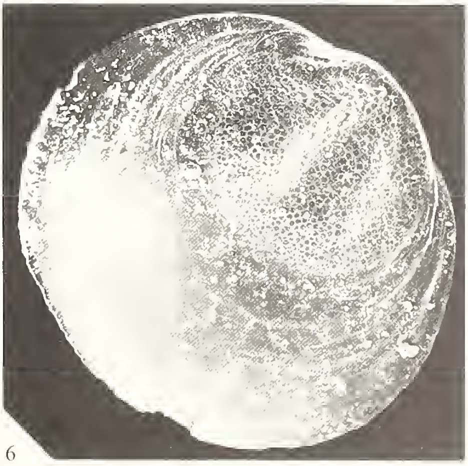
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POPOV *et al.*, *Opsiconidion*

TABLE 1. Statistics for ten dorsal valves of *Opsiconidion praecursor* sp. nov., from the Viljandi core (lower Pirgu Stage; depth 308·7 m and 310·1 m). Measurements in mm. Location of measurements as in Text-figure 3.

	Vector of Means					
	L	W	Iw	Pw	Sm	Sa
	0·42	0·47	0·18	0·08	0·28	0·36
	Variance–covariance matrix					
L	0·008					
W	0·0065	0·008				
Iw	0·002	0·002	0·002			
Pw	0·001	0·001	0	0		
Sm	0·004	0·004	0·001	0·001	0·004	
Sa	0·005	0·005	0	0·001	0·003	0·005

pseudointerarea, and a more centrally placed maximum height of the dorsal median septum. Moreover, the mean size (length and width) of *O. praecursor* is about half that of *O. aldridgei*. *O. praecursor* is also distinguished from all other species of the genus by having large larval pits surrounded by clusters of minute ones; all other species seem to have only one size of pits, usually showing cross-cutting relationships (e.g. Bitter and Ludvigsen 1979; Cocks 1979; Popov 1981). In this respect it is similar to species of *Biernatia* (Holmer 1986, 1989).

Williams and Holmer (1992) suggested that radial sets of 'drapes' identical to those described above are formed due to stresses in the outer mantle lobe induced by the setal muscles.

Family EPHIPPELASMATIDAE Rowell, 1965

[*nom. trans.* Popov and Holmer, herein (*ex* Ephippelasmatinae Rowell, 1965, p. H279)]

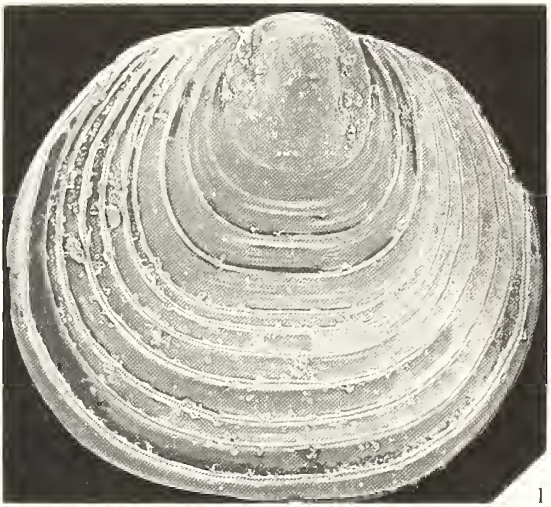
Diagnosis. Shell with narrow, straight posterior margin; larval shell with unequally distributed pits of varying size. Ventral valve recurved conical; ventral pseudointerarea catacline to strongly apsacline with intertrough; foramen within larval shell, usually forming external tube; internal pedicle tube usually present along posterior slope; apical process reduced, usually forming low ridge near apex. Dorsal valve slightly convex to concave; dorsal pseudointerarea divided by short, lens-like median groove; dorsal median septum variably developed; median buttress commonly absent.

Genera assigned. See Holmer (1986, p. 112; 1989, p. 112).

EXPLANATION OF PLATE 4

Figs 1–8. *Rhinotreta laeta* sp. nov. 1, Br 1639; depth 310·3 m; dorsal exterior; × 100. 2, Br 1640; depth 311·3 m; dorsal exterior; × 200. 3, Br 1635; depth 310·3 m; detail of ventral exterior, showing possible predatory borehole penetrating the larval shell; × 260. 4, detail of shell shown in fig. 3, showing edge of larval shell; × 1120. 5, detail of larval pitting of shell shown in fig. 3; × 5600. 6, Br 1638; depth 310·8 m; oblique posterior view of the ventral larval shell; × 310. 7, Br 1641; depth 310·3 m; ventral interior; × 330. 8, Br 1637; depth 309·1 m; ventral interior; × 360.

All scanning electron micrographs of specimens from the Upper Ordovician Pirgu Stage of the Viljandi core, Estonia.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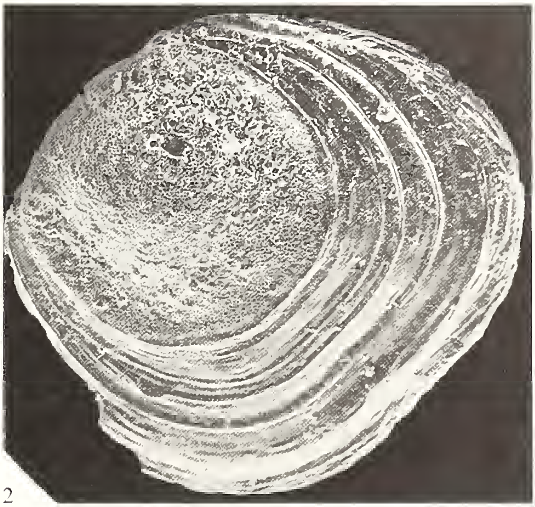
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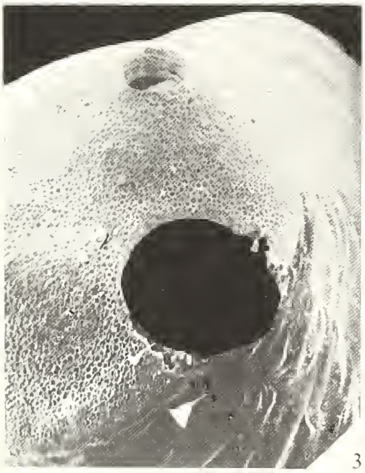
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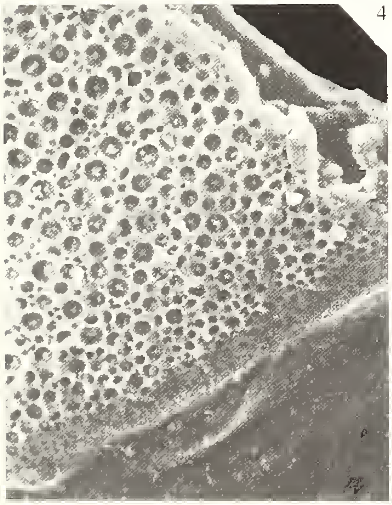
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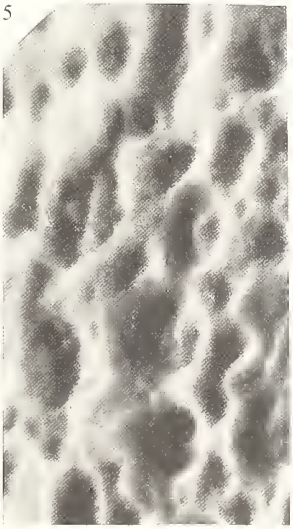
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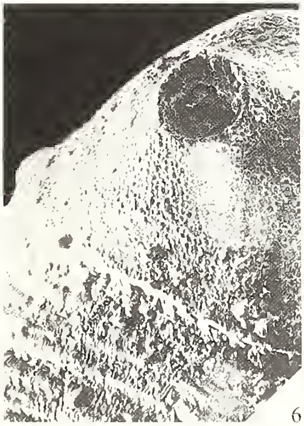
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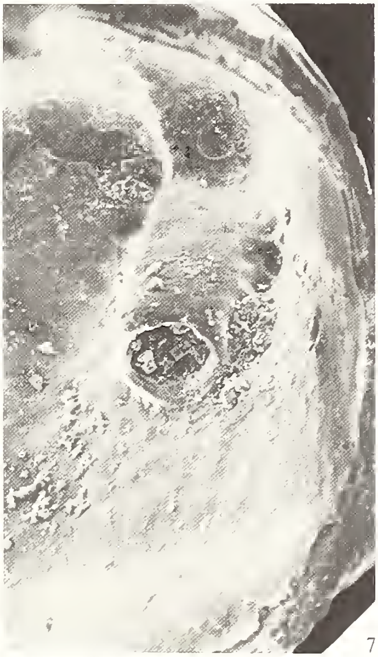
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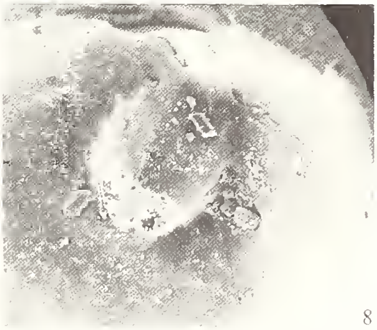
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POPOV *et al.*, *Rhinotreta*

Genus RHINOTRETA Holmer, 1986

Type species. By original designation; *Rhinotreta muscularis* Holmer, 1986, from the upper Viru Series, Gullhögen quarry, Västergötland, Sweden.

Diagnosis. Shell subcircular to subquadrate in outline. Ventral valve with long exterior pedicle tube. Dorsal valve flat, with low median ridge or septum.

Species assigned. Rhinotreta muscularis Holmer, 1986; *Rhinotreta davidi* Holmer, 1989; *Rhinotreta laeta* sp. nov.

Rhinotreta laeta sp. nov.

Plate 4; Plate 5, figures 1–4; Text-figure 4

1982 *Viljandia laeta* Popov *et al.*, p. 95, pl. 1, figs 5–6 [*nomen nudum*].

Derivation of name. Latin *laetus*, pleasant.

Type material. Holotype. Br 1634; complete shell (dorsal and ventral valves separated during preparation), from the Vormsi Stage, Viljandi core (depth 312·5 m), Estonia. Paratypes. Two complete shells, fifty five ventral and fifty three dorsal valves; Br 1635–1636, 1638–1640, 1642 are figured.

Diagnosis. Shell subquadrate in outline; ventral valve about 80–90 per cent as high as long; ventral pseudointerarea catacline to apsacline, bisected by indistinct intertrough; internal pedicle tube well developed. Dorsal valve flattened with raised umbo; dorsal pseudointerarea narrow, occupying about half of valve width.

Description. Shell subquadrate in outline (Pl. 4, figs 1–2), on average 87 per cent (s 8·8, N. 25) as long as wide. Ventral valve highly conical (Pl. 5, fig. 1), on average 88 per cent (s 17, N 17) as high as long. In lateral profile, the anterior slope of the valve is strongly and unevenly convex; the lateral slopes are evenly convex in transverse profile. Ventral pseudointerarea catacline to apsacline, with poorly developed, shallow intertrough (Pl. 5, fig. 1). Ventral interior with short pedicle tube along the posterior slope of the valve, supported by small, ridge-like apical process; the pedicle tube is covered by irregular polygonal pits, and the apical pits are placed directly lateral to the pedicle tube (Pl. 4, fig. 7).

Dorsal valve nearly flat with raised umbo. Dorsal pseudointerarea narrow, occupying on average 50 per cent (s 4·8, N 20) of the valve width; the median groove is gently concave, occupying on average 51 per cent (s 9·7, N 20) of the width of the pseudointerarea (Pl. 5, figs 2–3). Dorsal interior with large, but poorly defined

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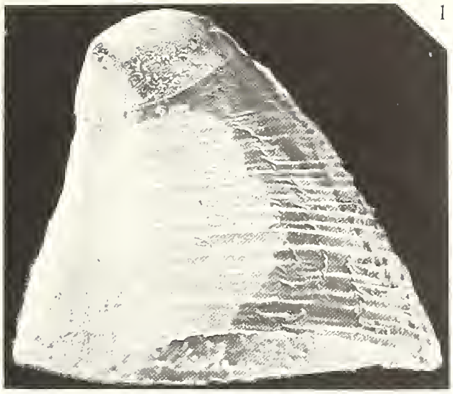
EXPLANATION OF PLATE 5

Figs 1–4. *Rhinotreta laeta* sp. nov. 1, Br 1634, holotype; Vormsi Stage; depth 312·5 m; oblique lateral view of ventral exterior (the dorsal and ventral valves of the complete shell were separated before photography); × 100. 2, oblique lateral view of dorsal interior of shell shown in fig. 1; × 130. 3, Br 1642; lower Pirgu Stage; depth 310·9 m; dorsal interior; × 100. 4, Br 1636; lower Pirgu Stage; depth 311·3 m; detail of pitted dorsal larval micro-ornament; × 1120.

Figs 5–10. *Scaphelasma scutula* sp. nov.; lower Pirgu Stage. 5, Br 1653 holotype; depth 308·7 m; lateral view of complete shell; × 75. 6, detail of pedicle opening of shell shown in fig. 5; × 330. 7, Br 1652; depth 311·3 m; lateral view of dorsal interior; × 100. 8, detail of structure of shell shown in fig. 7; × 420. 9, Br 1654; depth 311·3 m; dorsal exterior of shell shown in fig. 7; × 50. 10, detail of larval portion of shell shown in fig. 7; × 150.

All scanning electron micrographs of specimens from the Upper Ordovician of the Viljandi core, Estonia.

PLATE 5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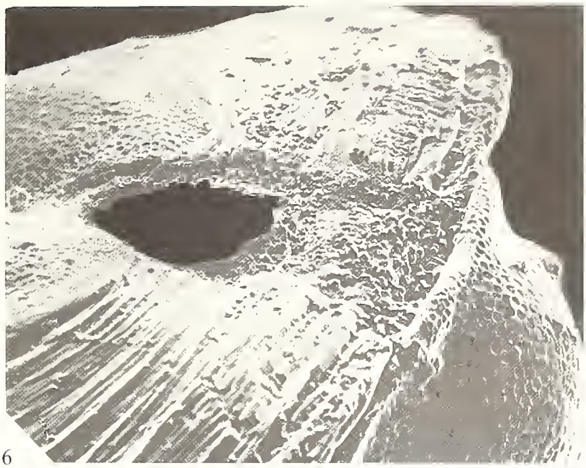
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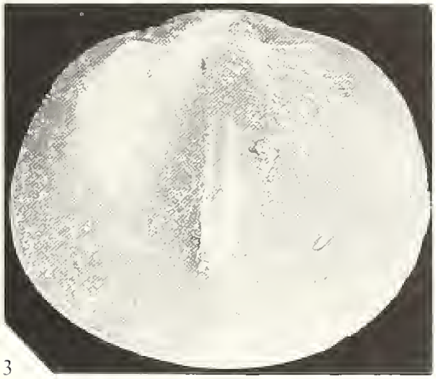
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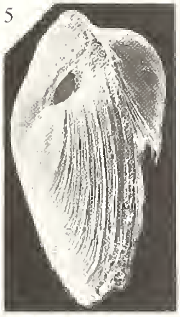
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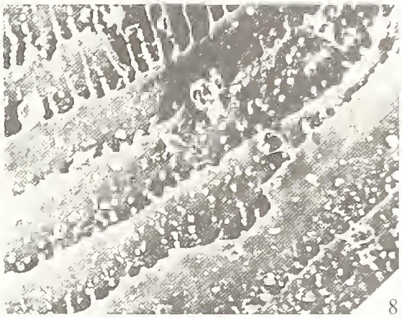
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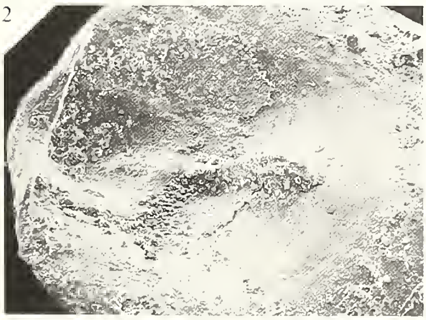
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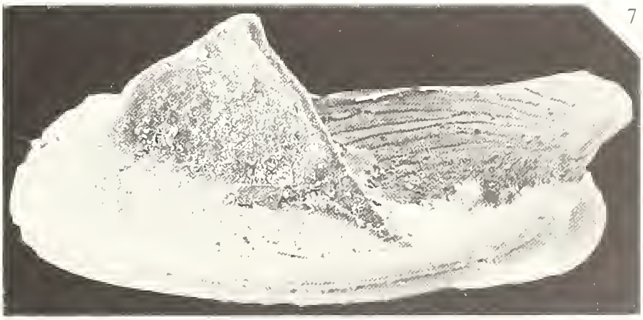
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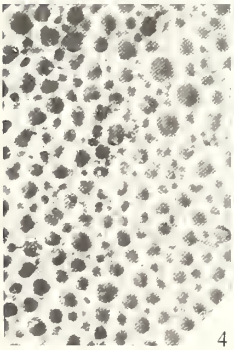
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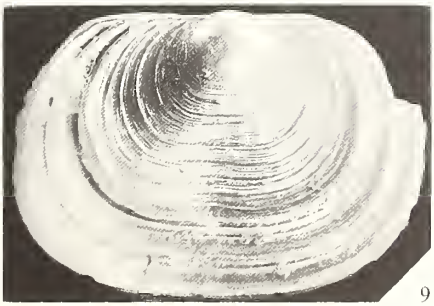
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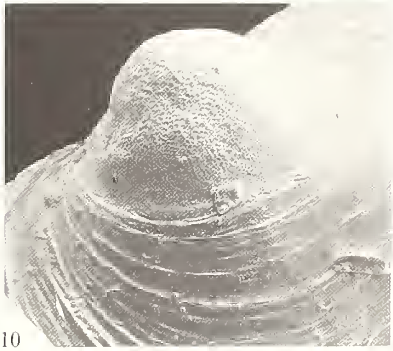
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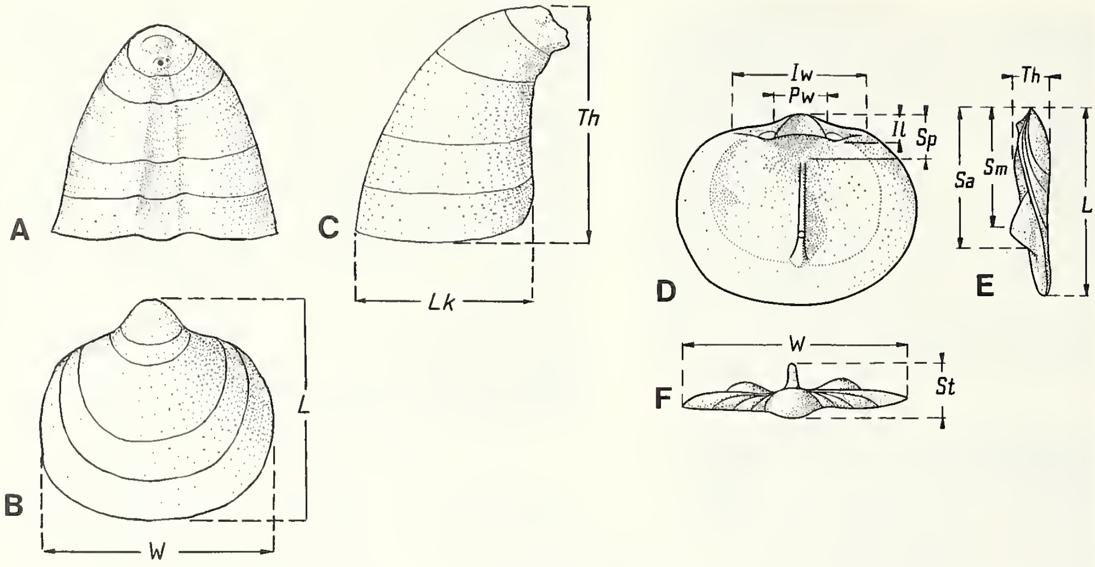
POPOV *et al.*, *Rhinotreta*, *Scaphelasma*



TEXT-FIG. 4. *Rhinotreta laeta* sp. nov. A–C, dorsal, and D–F, ventral valves, showing locations of measurements (Tables 2–3). See Text-figure 3 for legend.

TABLE 2. Statistics for ventral valves of *Rhinotreta laeta* sp. nov., from the Viljandi core. Measurements in mm. Location of measurements as in Text-figure 4.

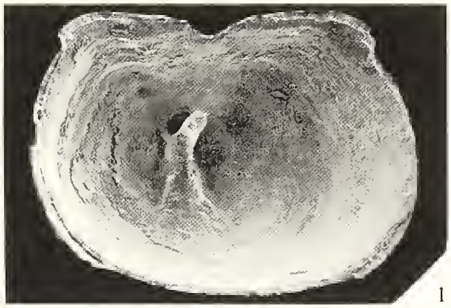
	(Depth 310·1 m, N 25)					(Depth 310·9 m, N 18)			
	Vector of Means					Vector of Means			
	L	W	Th	Lk		L	W	Th	Lk
	0·46	0·46	0·40	0·40		0·50	0·54	0·43	0·46
	Variance–covariance matrix					Variance–covariance matrix			
L	0·011				L	0·009			
W	0·011	0·013			W	0·009	0·006		
Th	0·013	0·014	0·016		Th	0·007	0·006	0·011	
Lk	0·007	0·008	0·010	0·0065	Lk	0·006	0·005	0·0065	0·0065

EXPLANATION OF PLATE 6

Figs 1–4. *Scaphelasma scutula* sp. nov.; Viljandi core (1, 4), Eikla core (2–3). 1, Br 1656; lower Pirgu Stage; depth 310·9 m; ventral interior; × 90. 2, Br 1651; Nabala Stage; depth 285·9 m; dorsal interior; × 100. 3, oblique anterior view of shell shown in fig. 2; × 100. 4, Br 1655; lower Pirgu; depth 310·9 m; ventral exterior; × 65.

Figs 5–10. *Eoconulus semiregularis* Biernat, 1973; lower Pirgu Stage. 5, Br 1657; depth 310·3 m; lateral view of dorsal exterior; × 100. 6, Br 1660; depth 310·9 m; ventral exterior; × 50. 7, detail of attachment scar of shell shown in fig. 6; × 300. 8, Br 1659; depth 311·3 m; ventral exterior; × 50. 9, Br 1664; depth 308·7 m; ventral exterior; × 50. 10, detail of attachment scar of shell shown in fig. 9; × 250.

All scanning electron micrographs of specimens from the Upper Ordovician of Estonia.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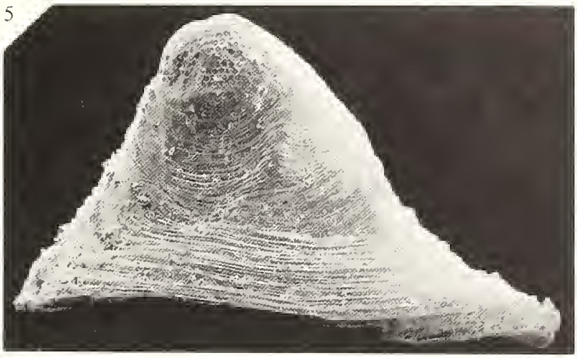
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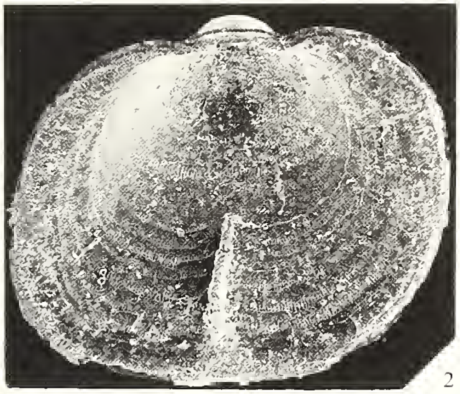
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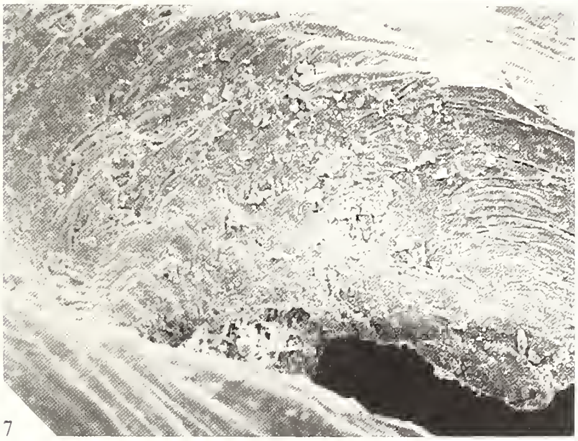
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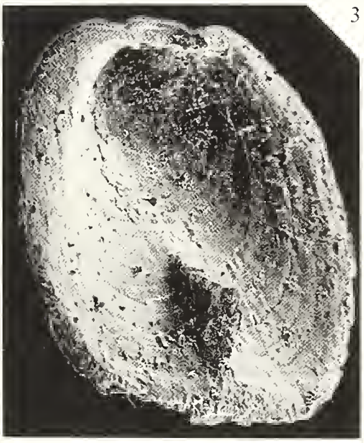
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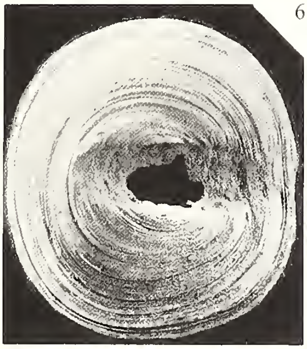
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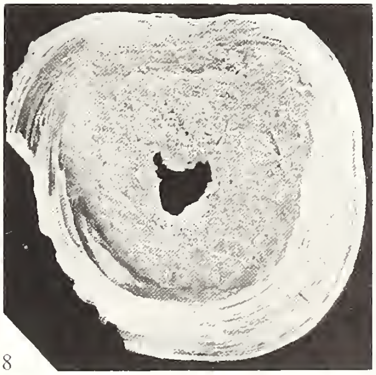
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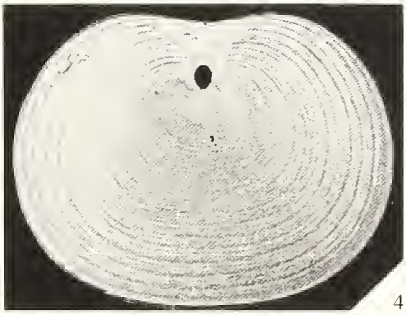
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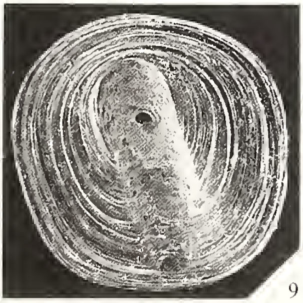
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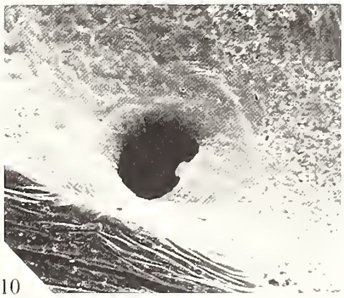
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TABLE 3. Statistics for eighteen dorsal valves of *Rhinotreta laeta* sp. nov., from the Viljandi core (lower Pirgu Stage; depth 310·1 m). Measurements in mm. Location of measurements as in Text-figure 4.

Vector of Means

L	W	Th	Il	Iw	Pw	Sp	Sm	Sa	St
0·62	0·72	0·09	0·07	0·36	0·19	0·18	0·34	0·45	0·13

Variance–covariance matrix

L	0·008									
W	0·011	0·020								
Th	0·001	0·003	0·001							
Il	0·001	0·001	0	0						
Iw	0·005	0·010	0·001	0·001	0·001					
Pw	0·003	0·005	0·001	0·001	0·003	0·003				
Sp	0	0	0	0	0	0	0·001			
Sm	0·002	0·005	0	0	0·001	0	0	0·001		
Sa	0·004	0·007	0·001	0·001	0·004	0·002	0	0·001	0·004	
St	0·003	0·004	0·0005	0	0·002	0·001	0	0	0·002	0·0015

cardinal muscle scars; dorsal median septum low, triangular, originating on average 33 per cent (s 7·8, N 17) of the valve width from the posterior margin, and extending for 60 per cent (s 7·8, N 17) of the length (Pl. 5, figs 2, 3). Valves ornamented by closely spaced, ridge-like, filae or lamellae; those of the dorsal valve are more widely spaced (Pl. 4, figs 1–2).

Discussion. *Rhinotreta laeta* differs from the other two described species, in having a more subquadrate outline, an ornamentation with high, ridge-like filae or lamellae, and a greater maximum size. It also differs from the type species *R. muscularis* in having a shorter external pedicle tube. It is distinguished from *R. davidi* by the poorly defined intertrough and somewhat shorter and higher dorsal median septum.

Family SCAPHELASMATIDAE Rowell, 1965

[*nom. trans.* Popov and Holmer, herein (*ex* Scaphelasmatinae Rowell, 1965, p. H278)]

Genus SCAPHELASMA Cooper, 1956

Type species. By original designation; *Scaphelasma septatum* Cooper, 1956, from the middle Ordovician of Alabama.

Scaphelasma scutula sp nov.

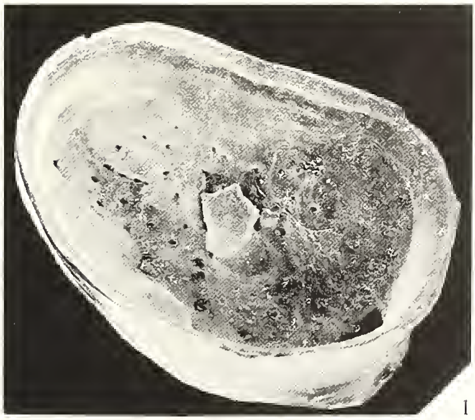
Plate 5, figures 5–10; Plate 6, figures 1–4; Text-figure 5

Derivation of name. Latin *scutula*, small plate.

EXPLANATION OF PLATE 7

Figs 1–7. *Eoconulus semiregularis* Biernat, 1973. 1, Br 1661; lower Pirgu Stage; depth 310·1 m; ventral interior; × 50. 2, detail of apical process of shell shown in fig. 1; × 200. 3, Br 1658; lower Pirgu Stage; depth 310·9 m; dorsal exterior; × 100. 4, detail of larval portion of shell shown in fig. 3; × 330. 5, detail of larval pitting of shell shown in fig. 3; × 940. 6, Br 1662; Vormsi Stage; depth 312·5 m; juvenile dorsal exterior; × 200. 7, lateral view of shell shown in fig. 6; × 235.

All scanning electron micrographs of specimens from the Upper Ordovician of the Viljandi core, Estonia.



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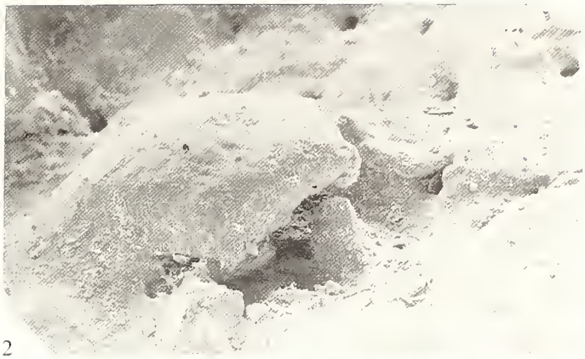

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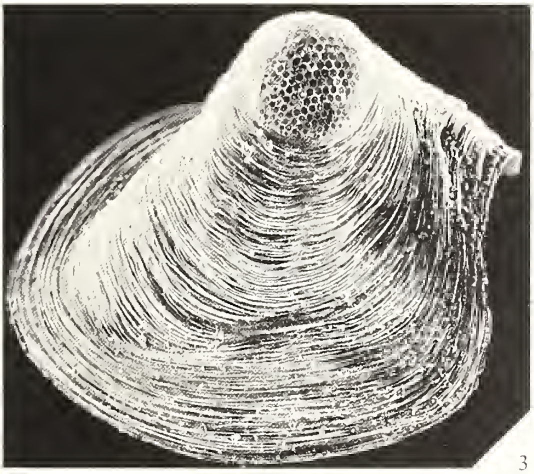

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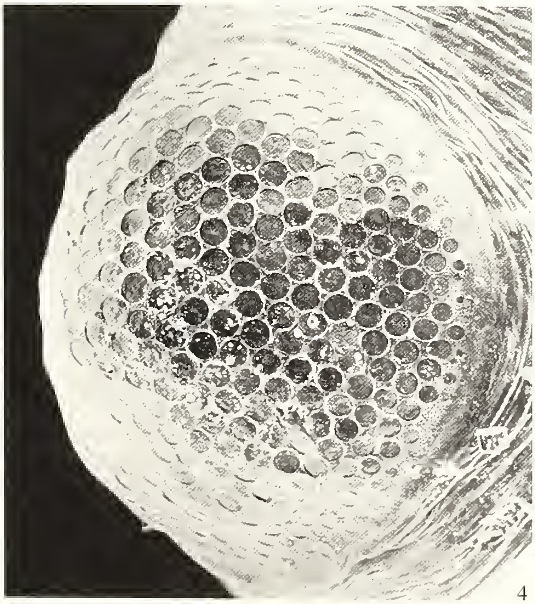

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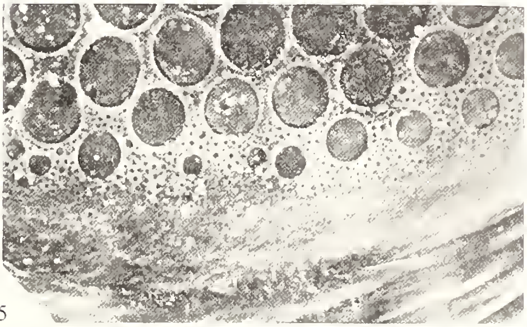

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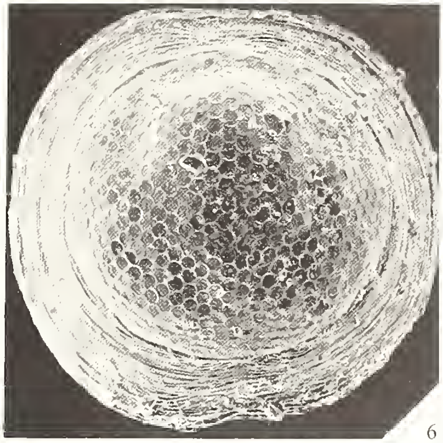

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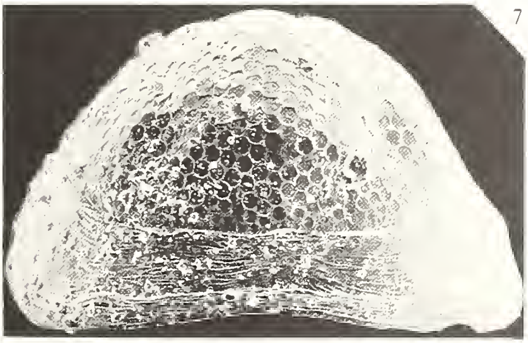


7

POPOV *et al.*, *Eoconulus*

Type material. Holotype. Br1653, complete shell, from the Vormsi Stage of the Viljandi core (depth 308·7 m), Estonia. Paratypes. Three complete shells, twenty ventral and twenty dorsal valves; Br 1651–1652, 1654–1656 are figured.

Diagnosis. Ventral interior with apical process forming a rod-like projection directly anterior of pedicle opening.

Description. Shell transversely oval in outline. Ventral valve widely conical, on average 83 per cent (s 3·9, N 12) as long as wide, and 48 per cent (s 1.2, N 13) as high as long; the maximum height is placed on average 36 per cent (s 3·2, N 13) of the valve length from the slightly concave posterior margin. Ventral pseudointerarea strongly procline with well defined intertrough (Pl. 6, fig. 4). Pedicle foramen elongately oval, about 60 μm long and 40 μm wide (Pl. 5, fig. 6). Apical process forming rod-like projection, placed directly in front of the pedicle opening (Pl. 6, fig. 1).

Dorsal valve strongly convex in apical region, flattening marginally; on average 86 per cent (s 7·2, N 19) as long as wide (Pl. 5, figs 9–10). Dorsal pseudointerarea narrow, occupying on average 23 per cent (s 4·0, N 18) of the valve width; median groove lens shaped, slightly concave, occupying on average 43 per cent (s 12, N 18) of the width of the pseudointerarea (Pl. 6, figs 2–3). Dorsal interior with high, triangular median septum occupying starting on average 48 per cent (s 11, N 19) of the valve length from the posterior margin and extending for 88 per cent (s 5·0, N 18) of the length; the maximum height is placed at 72 per cent (s 7·4, N 18) of the valve length from the posterior margin (Pl. 5, fig. 7; Pl. 6, figs 2–3).

Discussion. *Scaphelasma scutula* differs from all other known species of the genus in having a well developed, rod-like apical process.

Family EOCONULIDAE Cooper, 1956
Genus EOCONULUS Cooper, 1956

Type species. By original designation; *Eoconulus rectangulatus* Cooper, 1956, from the middle Ordovician of Alabama.

Eoconulus semiregularis Biernat, 1973
Plate 6, figures 5–10; Plate 7; Text-figure 6

1973	*Eoconulus semiregularis* sp. nov. Biernat, p. 112, pl. 36, figs 1–8.
1982	*Eoconulus semiregularis* Biernat; Popov *et al.* p. 101, pl. 2, fig. 6.
?1989	*Eoconulus* cf. *semiregularis* Biernat; Holmer, p. 150, figs 39I, 106–107, 111.

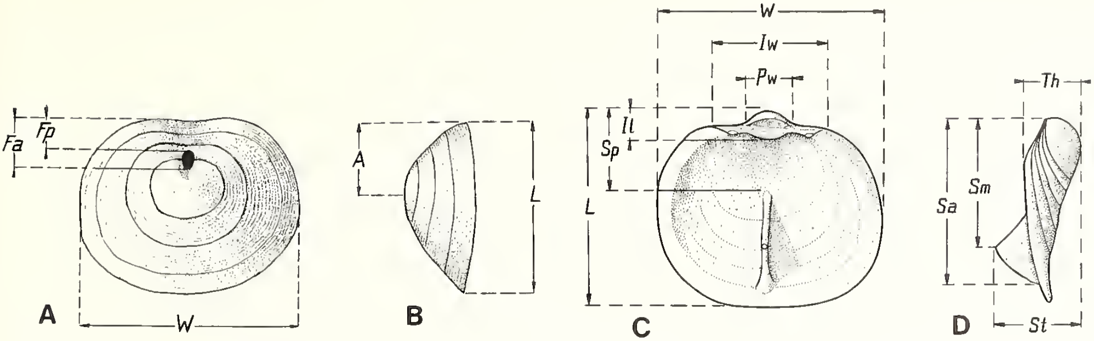
Holotype. Bp VI/6*b* (dorsal valve; in the Palaeobiological Institute, Polish Academy of Sciences, Warszawa), from an Upper Ordovician erratic boulder (no. 0·247). Jarosławiec, Baltic coast, Poland.

Material. Four ventral and eighty six dorsal valves; Br 1657–1658, 1660–1662, 1664 are figured.

Diagnosis. Shell irregularly subcircular in outline. Dorsal valve usually highly conical. Ventral valve truncatedly cylindrical in profile, with large, flattened to irregularly shaped, or cylindrical attachment scar; ventral interior with well developed apical process directly anterior to pedicle opening.

Description. Ventral valve truncate-cylindrical in profile. Attachment scar commonly forming a mould of a cylindrical object, more rarely flat or irregular (Pl. 6, figs 6–9). Pedicle foramen small, circular, about 40 μm in diameter, placed at about the centre of the attachment scar (Pl. 6, fig. 10). Ventral interior has a wart-like apical process, slightly overhanging the internal pedicle opening; three or five 'papillae' surround the apical process (Pl. 7, fig. 2). Ventral cardinal muscle scars strongly raised. Ventral interior surface with deep, cylindrical pores that do not reach the external valve surface (Pl. 7, figs 1–2).

Dorsal valve usually highly conical, on average 93 per cent (s 13, N 24) as long as wide and 68 per cent



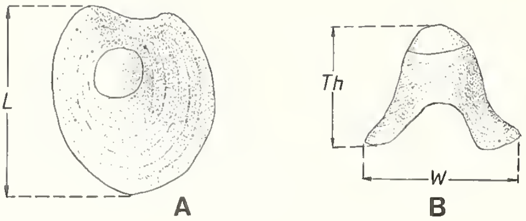
TEXT-FIG. 5. *Scaphelasma scutula* sp. nov. A–B, dorsal, and C–D, ventral valves, showing locations of measurements (Tables 4–5). See Text-figure 3 for legend.

TABLE 4. Statistics for thirteen ventral valves of *Scaphelasma scutula* sp. nov., from the Viljandi core (Vormsi–lower Pirgu stages; depth from 308·7 to 312·5 m). Measurements in mm. Location in mm. Location of measurements as in Text-figure 5.

	L	W	Th	Fp	Fa	A
Vector of means	0·66	0·79	0·32	0·13	0·18	0·24
Variance–covariance matrix						
L	0·022					
W	0·026	0·038				
Th	0·014	0·019	0·013			
Fp	0·0085	0·011	0·005	0·004		
Fa	0·008	0·010	0·005	0·0035	0·004	
A	0·007	0·009	0·004	0·003	0·003	0·003

TABLE 5. Statistics for sixteen valves of *Scaphelasma scutula* sp. nov., from the Viljandi core (Vormsi–lower Pirgu stages; depth from 308·7 to 312·5 m). Measurements in mm. Location of measurements as in Text-figure 5.

	L	W	Th	Il	Iw	Pw	Sa	Sm	Sp	St
Vector of means	0·61	0·72	0·13	0·075	0·32	0·14	0·54	0·44	0·27	0·22
Variance–covariance matrix										
L	0·022									
W	0·033	0·052								
Th	0·002	0·004	0·001							
Il	0·003	0·004	0	0·001						
Iw	0·016	0·016	0·0015	0·002	0·018					
Pw	0·0075	0·007	0·001	0·001	0·006	0·003				
Sa	0·024	0·033	0·003	0·003	0·017	0·007	0·026			
Sm	0·016	0·022	0·002	0·002	0·012	0·006	0·013	0·013		
Sp	0·001	0·003	0	0	0·001	0	0·001	0·001	0·001	
St	0·015	0·015	0·001	0·002	0·010	0·005	0·014	0·012	0·001	0·010



TEXT-FIGURE. 6. *Eoconulus semiregularis* Biernat, 1973. Dorsal valve, showing locations of measurements (Table 6). See Text-figure 3 for legend.

TABLE 6. Statistics for twenty four dorsal valves of *Eoconulus semiregularis* Biernat, from the Viljandi core (lower Pirgu Stage; interval 310·1–311·3 m). Measurements in mm. Location of measurements as in Text-figure 6.

Vector of Means

L	W	Th	A
0·78	0·85	0·53	0·22

Variance–covariance matrix

L	0·067			
W	0·076	0·112		
Th	0·041	0·045	0·037	
A	0·025	0·025	0·017	0·018

(s 9·8, N 24) as high as long. The maximum height is placed on average 28 per cent (s 12, N 25) of the valve length from the posterior margin (Pl. 6, fig. 5). Dorsal interior lacking distinctive features.

The dorsal larval shell is about 0·2 mm in diameter, ornamented by two grades of pits; the larger ones are flat-bottomed, 9·0–10·0 μm in diameter, separated from one another by flattened ridges that are covered by clusters of minute pits, 0·3–0·6 μm in diameter (Pl. 7, fig. 4). Towards the edge of the larval shell, the diameter of the larger pits decreases to 2·3–7·4 μm and the finer pits increase in number; outside of this zone, the larval shell is surrounded by a band, 12–15 μm wide, ornamented only by minute pits (Pl. 7, fig. 5). The ventral larval shell is not defined; the attachment scar is ornamented only by fine, concentric filae (Pl. 6, fig. 7).

Discussion. As noted by Holmer (1989), it is difficult to make meaningful definitions of species of *Eoconulus*, since the outline and convexity of the valves are almost completely dependent upon the shape of the substrate. Moreover, most described species of the genus are known only from the dorsal valve, as is the case with the Polish type material of *E. semiregularis*. However, the dorsal valves in the Estonian material are identical to the Polish specimens in all available characters. Our material is also closely comparable with *E.* cf. *semiregularis* Biernat described by Holmer (1989) from the mid-Ordovician of Sweden, but the Estonian dorsal valves have a higher dorsal valve and a greater maximum size.

Order DISCINIDA Waagen, 1885
Family DISCINIDAE Gray, 1840
Genus SCHIZOTRETA Kutorga, 1848

Type species. By original designation; *Orbicula elliptica* Kutorga, 1846, from the Lower Ordovician of Ingria, St Petersburg district, Russia.

Schizotreta sp.

Plate 1, figures 8–9

Material. Two ventral and six dorsal valves; Br 1631, Br 1632 are figured.

Remarks. There are only a few specimens of *Schizotreta* in the collection, none of which allows a specific determination. They are, however, very similar to *S. concava* Wright, 1963, in having the dorsal apex placed close to the posterior margin and ornamentation with coarse, ridge-like, concentric filae.

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TRUE *STROPHOMENA* AND A REVISION OF THE CLASSIFICATION AND EVOLUTION OF STROPHOMENOID AND 'STROPHODONTOID' BRACHIOPODS

by RONG JIA-YU *and* L. R. M. COCKS

ABSTRACT. The brachiopod superfamily Strophomenoidea is reviewed and reclassified, with chief emphasis on the form and evolution of the cardinalia, the denticulation, the ventral muscle fields, and the dorsal side septa. There are six families without denticulation along the hinge line: the Christianiidae, Foliomenidae, Glyptomenidae, Leptaenoideidae, Rafinesquinidae, and Strophomenidae; and seven families with denticles along the hinge line: the Amphistrophiidae, Douvillinidae, Eopholidostrophiidae, Leptostrophiidae, Shaleriidae, Strophodontidae and Strophonellidae. A separate superfamily 'Strophodontacea' is not recognized since denticulation arose polyphyletically, mainly from different stocks within the Rafinesquinidae. Experimentation in the development of denticles and crenulations in the Strophomenidae, Leptaeninae and other groups also occurred but was unsuccessful. The form of the cardinalia is the most important character for differentiating families apart from the later denticulate genera, in which parallel evolution of the cardinalia occurred, and the form of the ventral valve muscle field and other structures are used. A lectotype is selected for *Strophomena planumbona*, the type species of *Strophomena*, and the new genus *Palaeoleptostrophia* is erected, with type species *Stropheodonta jamesoni*, from the lower Llandovery (Rhuddanian) of Girvan, Scotland. *Brachyprion*, *Eostropheodonta*, *Leptaena*, *Rhenostrophia*, and associated genera are revised, and the new family Eopholidostrophiidae is erected.

WHILST undertaking synoptic work for the revised brachiopod volume of the *Treatise on invertebrate paleontology*, we realized that the classification of the strophomenoid genera within subfamilies, families and superfamilies required fundamental revision. The group includes the key genera *Strophomena* and *Leptaena*, which at the time of their erection in the early nineteenth century were thought to encompass a wide range of brachiopods. Thus for example, in Davidson's great monograph on the fossil brachiopods of Britain (1871, pls 39–49), the illustrations of '*Strophomena*' figured forms now included in *Amphistrophia*, *Brachyprion*, *Christiania*, *Colaptomena*, *Coolinia*, *Dactylogonia*, *Eostropheodonta*, *Eostrophonella*, *Gunnarella*, *Isophragma*, *Katastrophomena*, *Kiaeromena*, *Lepidoleptaena*, *Leptaena*, *Leptostrophia*, *Mackerrovia*, *Macrocoelia*, *Megastrophia*, *Mesopholidostrophia*, *Morinorhynchus*, *Oepikina*, *Pentlandina*, *Ptychoglyptus*, *Rafinesquina*, *Shaleria*, *Strophomena*, and *Strophonella*; and the illustrations of '*Leptaena*' include brachiopods now assigned to *Bimuria*, *Christiania*, *Eoplectodonta*, *Kjaerina*, *Leangella*, *Mesopholidostrophia*, *Shagamella*, *Sowerbyella*, and *Sowerbyites* (Cocks 1978). What has happened since is that key groups, such as the Plectambonitoidea (including *Bimuria*, *Eoplectodonta*, *Isophragma*, *Leangella*, *Ptychoglyptus*, *Sowerbyella*, and *Sowerbyites* in the above list), with their distinctive simple, trifid or undercut cardinal processes as opposed to the bifid cardinal processes of the Strophomenoidea, have been separated from the main strophomenoid concept. Similarly, the chonetoids (including *Shagamella* above), with their spines along the ventral cardinal margin, have long been recognized as a separate suborder, as have also the orthotetoids, with their impunctate shells in Ordovician and Silurian forms (including *Morinorhynchus* and *Coolinia*).

Thus the reduced, but nevertheless abundant and important group, requires reclassification. In

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the past this has been done chiefly by grouping shell shapes and profiles together, with, for example the resupinate Strophomenidae, the convexo-concave Rafinesquinidae and the rugose Leptaenidae, but, as discussed below, these characters we consider to represent merely generic, rather than familial, differences. Today there are about two hundred and fifty nominal genera within the group, although we consider many to be subjective synonyms; nevertheless their logical allocation to appropriate groups of familial or greater or lesser rank, is one of the tasks that form the core of this paper. The other is to investigate the acquisition of denticles along the hinge line and thus to assess the true relationship between the strophomenoids and the 'strophodontoids'. After assessment of all the available characters, the morphology and the evolution of the cardinalia and of the denticulation have been found to be the two most important criteria. In this paper we use the term 'strophodontoid' to include all strophomenoids with denticles on the hinge line; however, this does not imply that we recognize the Strophodontoidea as a separate superfamily (see below).

HISTORY OF FAMILIAL CLASSIFICATION

From 1846, when King erected the Strophomenidae, attention has been caught by this conspicuous group of Palaeozoic brachiopods. In the nineteenth century the Strophomenidae were separated from the spiny chonetoids and productoids by the absence of external spines. In 1893 Schuchert distinguished the Rafinesquininae as a subfamily of the Strophomenidae on the basis of shell outline and profile, but this was published at the time that Hall and Clarke (1894) was in press, otherwise the latter would have been unlikely to have persisted with the erection of the Leptaenidae. In the present century, Jones (1928) separated the plectambonitoids on the basis of shell shape as a subfamily within the Strophomenidae, and Caster (1939) erected the subfamily Stropheodontinae (with the tribes Stropheodontini, Douvillinini and Leptostrophiini) and also the subfamily Strophonellinae for strophomenoids with denticles on their hinge lines; Stainbrook (1943) erected the Pholidostrophiinae within the latter. However, the first review with anything like a rational basis of division for the strophomenoids as a whole was that by Williams (1953*b*), who followed Öpik's earlier studies in recognizing the fundamental importance of the difference between the simple or trifid cardinal processes of the plectambonitoids and the bifid cardinal processes of the other groups and elevated the Strophomenacea, Plectambonitacea, and Orthotetacea to superfamilial rank. Williams recognized the importance of a cemented mode of life by erecting the Liljevalliinae and Leptaenoideinae as subfamilies and also distinguished the very individual Christianiidae as a family for the first time. Together with the Oepikininae previously erected by Sokolskaya (1960) and the Foliomenidae, Furcitellinae, Glyptomeninae, Leptodontellinae, and the Shaleriidae, all erected in the volume, this formed the classification used in Williams (1965). Shortly afterwards, Havlíček (1967) proposed the Eostropheodontidae and Elliptostrophiidae, together with numerous new genera, in his substantial monograph on the Strophomenida from Czechoslovakia and Harper (1973) erected the Amphistrophiinae. In 1976 Pope reviewed the Strophomenacea and erected a new subfamily Murinellidae and the tribe Teratelasmini within a new classification based on a complicated mixture of the perceived type of pseudopunctae, the overall shape, the dental lamellae and teeth, and, at a lower level the form of the cardinal process and other interior and exterior features.

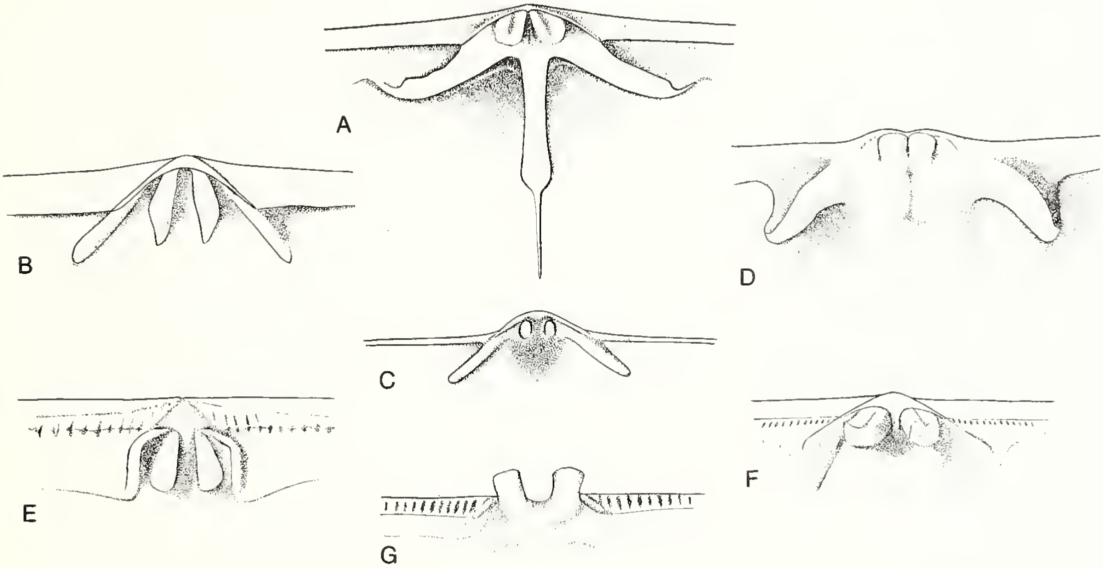
Sokolskaya (1960) had been the first to treat the forms with internal hinge denticles as a superfamily Stropheodontacea, separate from the superfamily Strophomenacea, and this was followed by various authors, but not by Williams (e.g. 1965), Cocks (1967, 1968) or Bassett (1971). Cocks (1978, p. 124) regarded the acquisition of denticles as polyphyletic and thus did not regard the Stropheodontacea as a valid monophyletic superfamily. Harper and Boucot (1978) reviewed what they termed the Stropheodontacea at length, with many new genera and nine new families and subfamilies, namely the Brachyprioninae, Douvillinellinae, Lissostrophiidae, Mesodouvillininae, Mesoleptostrophiinae, Nervostrophiinae, Protodouvillininae, Teichostrophiinae, and Telaeoshaleriidae. Since that time there has been a relative pause in activity, with only the family Maoristrophiidae

Ushatinskaya and Alekseeva (1983) and the subfamilies Megastrophiinae Jahnke (1981) and Dicoelostrophiinae Wang and Rong (1986) added to the list of over thirty available taxa of familial and subfamilial rank within the strophomenoids (not including the plectambonitoids and orthotetoids).

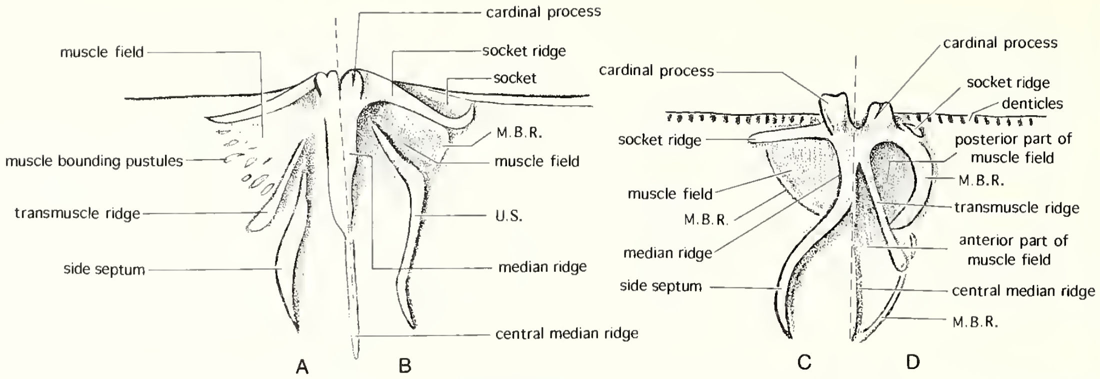
KEY MORPHOLOGICAL CHARACTERS

Cardinalia types

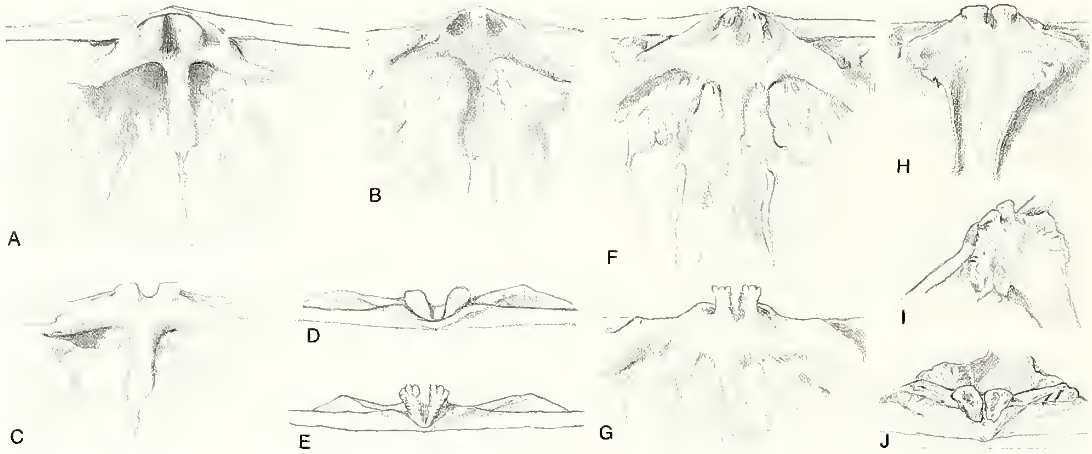
We have recognized four different types of cardinalia within the strophomenoids with smooth hinge lines, termed A to D on Text-figure 1 and the key to the terminology on Text-figure 2. The three chief differences are (a) the general shape of the cardinal process lobes, (b) their position relative to the hinge line and socket ridges, and (c) the attitude of the socket ridges and their relationship to the cardinal process lobes. The four types are (A) the *Strophomena* type (Pl. 1, fig. 7; Text-fig. 1A), which have robust and often oval cardinal process lobes situated on the posterior part of a notothyrial platform which is usually prominent. The process lobes can be discrete, but are sometimes fused together at the bases before merging with the notothyrial platform, as in *Oepikina* (Pl. 3, fig. 7). The cardinal process lobes are situated either upon the hinge line, or slightly postero-ventrally to it, and do not project anteriorly to any large degree. In addition, in many genera the socket ridges are curved posterolaterally – a feature not seen in any other cardinalia type. Type B is shown by *Kjerulfina* (Text-fig. 1B) and *Kjaerina* (Pl. 3, figs 1–5), in which the cardinal process lobes are elongate or plate-like in shape and remain entirely discrete throughout ontogeny. Most of the lobes are situated anterior to the hinge line, extending even as far as the anterior ends of the socket ridges. The notothyrial platform is variably developed; sometimes, e.g. *Kjerulfina*, it is absent and in other genera, such as in some species of *Kjaerina* (Pl. 3, fig. 2) and *Rafinesquina* (Pl. 2, fig. 5), it is well developed. The socket ridges are straight and usually smaller than in Type A, and were more important in the early growth stages of some genera; for example, in *Leptaena rugosa* the smaller specimens (Pl. 4, fig. 4; Text-fig. 4) have more prominent socket ridges



TEXT-FIG. 1. The seven types of strophomenoid cardinalia. Type A, based on *Strophomena*; Type B, based on *Kjerulfina*; Type C, based on *Bystromena*; Type D, based on *Christiania*; Type E, based on *Leptostrophia*; Type F, based on *Amphistrophia*; Type G, based on *Strophodonta*.



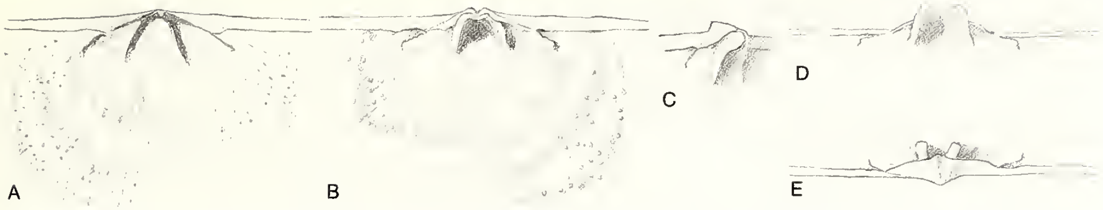
TEXT-FIG. 2. Strophomenoid dorsal valve morphology, showing the terminology used here. A, *Dactylogonia*; B, *Quondongia*; C, *Protodouvillina*; D, *Malurostrophia*. M.B.R., muscle bounding ridge; U.S., united structure of transmuscle ridge and side septum.



TEXT-FIG. 3. Cardinalia typical of the family Strophomenidae. A–D, *Strophomena planumbona*, based on AMNH 918/5. E–G, *Murinella partita* Cooper, based on USNM 117640. H–J, *Biparetis paucirugosus* Amsden, based on OGS 6716; all × 3.

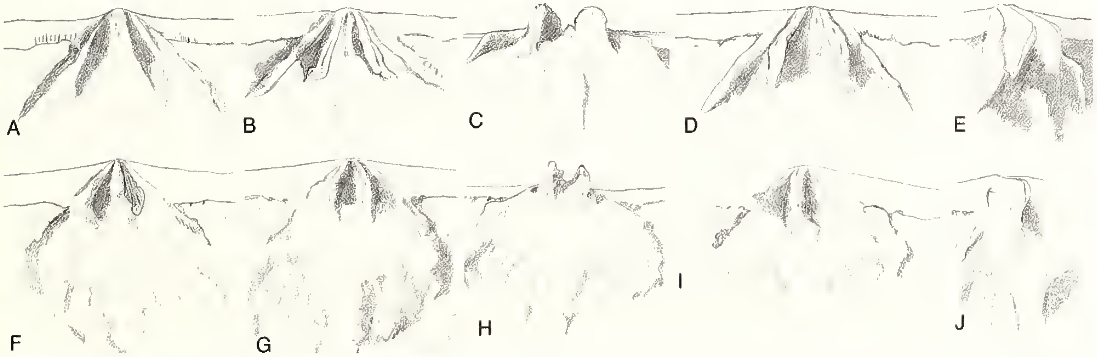
than the gerontic individuals (Pl. 4, fig. 2). In a few extreme genera, for example *Rafinesquina* itself, the cardinal process lobes are extremely strong and ponderous and dwarf the socket ridges in size (Pl. 2, figs 1–7; Text-fig. 2). The cardinalia of Type C are delicate, such as those in *Paromalomena* and *Bystromena* (Text-figs 1C, 6), with small cardinal process lobes on or largely posterior to the hinge line. The socket ridges are directly fused in some cases to the bases of cardinal process lobes. There is usually no notothyrial platform. There is often a concave area immediately anterior to the cardinal process lobes. Type D has only been found in *Christiania* (= *Christianella* Liang) (Text-figs 1D, 7), in which the low cardinal process lobes are very close together and fused at their bases. The socket plates (note the use of the term 'plate' here rather than 'ridge' to emphasize their strength) are often elevated from the valve floor anteriorly.

There are three additional types of cardinalia in the 'strophodontoids', which we term E, F and G. However, many early stocks, such as *Eostrophonella* (Pl. 5, fig. 4), *Palaeoleptostrophia* gen. nov. (Pl. 4, fig. 8) and *Eostropheodonta* in the Ashgill and Llandovery, have Type B cardinalia. Type E is characterized by strong,



TEXT-FIG. 4. The cardinalia of a medium-size specimen of topotype *Leptaena rugosa*. A, internal mould. B–E, various views of latex cast; all based on BB 67946; ×6.

thick, plate-like cardinal process lobes directed ventrally and which are not developed posteriorly beyond the cardinal margin, such as in *Leptostrophia* (Pl. 7, fig. 6; Text-fig. 7). Socket ridges may be present but they are usually small and situated close to or postero-lateral to the cardinal process lobes, as in *Leptostrophia*, or absent, as in *Protoleptostrophia*. The cardinal process lobes are variably divergent and are sometimes even convergent onto a median ridge, as in *Mesoleptostrophia filosa* (Text-fig. 20). In Type F the cardinal process lobes are relatively small but swollen and knob-like and they are ventrally (not posteriorly) directed, as in *Amphistrophia striata* (Text-fig. 1F) and *Shaleria* (*Janiomya*) *ornatella* (Text-fig. 19). This type is seen mainly in later Silurian amphistrophiids and shaleriids, but has not been recorded in leptostrophiids. In Type G the cardinal process lobes are strong and posteriorly directed, as in *Strophodonta* itself (Pl. 7, fig. 5; Text-fig. 1G), and their bases may or may not be united. Type G is seen mainly in Devonian strophodontids and douvillinids, but seldom in leptostrophiids. Socket ridges are usually developed, but they are often short and even absent in *Pholidostrophia* and *Lissostrophia*. Type F was probably the ancestor of Type G and was probably derived in turn from Type B. Type E may also have been derived from Type B.

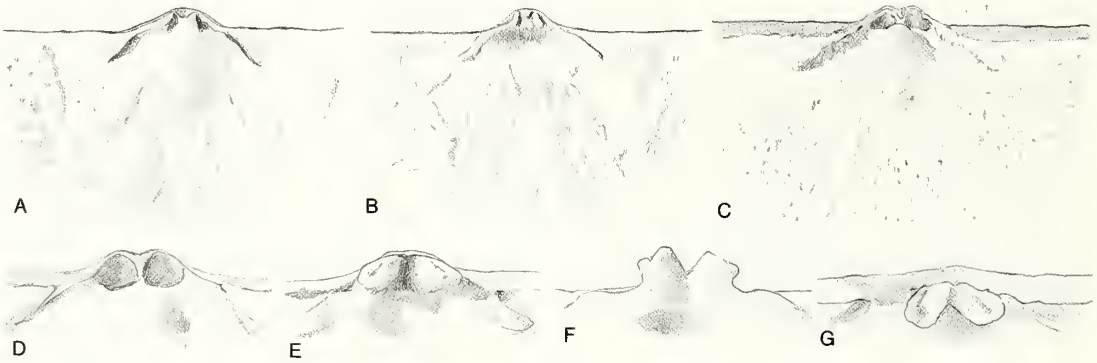


TEXT-FIG. 5. Cardinalia of A–E, *Eostrophonella eothen* based on BC 50617, compared with, F–J, *Kjerulfina polycyma* based on BB 73901; all ×6. In both series the chilidium is not shown.

Teeth, denticles, and crenulations

Most early brachiopods, particularly orthoids, have a simple articulation consisting of a pair of teeth in the ventral valve which interlocked with a pair of sockets in the dorsal valve. The sockets are negative features formed between the hinge at their posterior edge and a pair of plates or ridges, termed socket plates or socket ridges, at their anterior edge. Many early strophomenoids had this simple configuration of teeth and sockets. In contrast, some more advanced ‘strophodontoids’ had replaced the simple tooth and socket system by a number of denticles, which were spread along part or all of the hinge line of both valves to provide additional articulation. These denticles appeared for the first time in the latest Ordovician (Ashgill) in genera such as *Origostrophia* Mitchell, 1977.

However, between these two extreme forms of articulation there are a number of structures present in various strophomenoid genera whose function is difficult to interpret in detail, but whose general purpose was probably to make the articulation system more efficient. These structures take the form of a variety of regular or irregular striae found on various facets of the teeth and socket ridges, and also on anterior extensions of the hinge line, some of which form composite structures with the teeth. Various terminologies have been used to describe these structures and the striae occurring on them, for example Williams (1951, fig. 22) showed *Eostropheodonta* as possessing composite structures including dental plates and denticular plates, both of which carried what he termed denticles. However, in this paper we reserve the use of 'denticles' to include striae on the hinge lines only, or on anterior extensions in the same plane as, or just below, the hinge; the striae on the interior-facing teeth or socket ridges we term 'crenulations'. A particular variation arises when two different types of striae are seen on adjacent facets of the teeth, for example in *Biparetis* (Text-figs 8, 13), in which only the antero-median crenulations on the teeth intermesh with similar crenulations on the socket ridges; the finer striations on the posterior part have no counterparts in the dorsal valve. Striations may be regular, as in *Biparetis*, or irregular, as in *Strophomena* itself (Pl. 1, fig. 10), where striations bifurcate or coalesce and are often also sinuous. All 'strophodontoid' denticles are essentially regular, and we only attribute the term 'strophodontoid' to those strophomenoids with denticles on the hinge line. Crenulations and striations on the teeth and the sockets are common in many taxa of strophomenoids and have been observed by many authors (such as Spjeldnaes 1957, p. 20; Amsden 1974, p. 52; Pope 1976, p. 192; Harper and Boucot 1978; Harper *et al.* 1985, p. 300) although the developmental degree of these structures is different and in many genera they are absent. However, this has not created much attention. For example, *Eostropheodonta* and *Aphanomena*, both of which have crenulations and denticles (Text-fig. 8), have been ascribed to several different families – the Leptostrophiidae by Williams (1965), Eostropheodontidae by Havlíček (1967) and Rafinesquinidae by Bergström (1968). Even the species name *strophodontoides* has been questionably assigned to the genus *Rafinesquina* itself (Amsden 1974), although we attribute this taxon to *Eostropheodonta*.

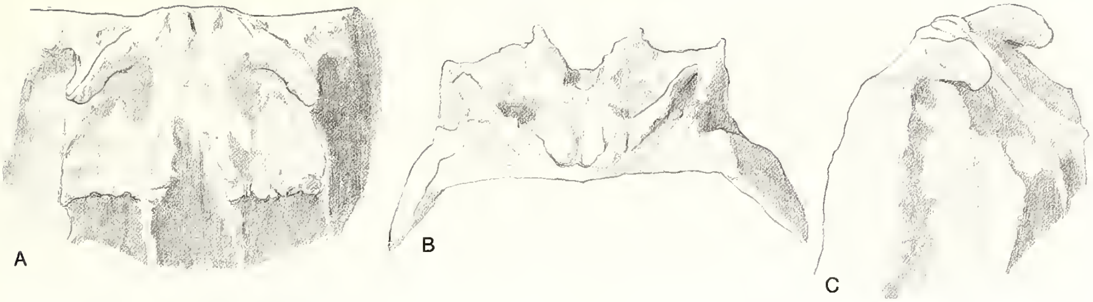


TEXT-FIG. 6. Cardinalia of Type C. A–B, *Bystromena perplexa* based on BB 35367; ×6. C–G, *Paromalomena polonica*; C, based on BB 29666 and D–G, on BB 29216; ×12.

Similar crenulations can be seen in several families, not all of which are closely related, and they are found in the strophomenoids listed in the Appendix. There can be great variation within a single population, and crenulations (although not strophodontoid denticles) can be present, feebly developed or absent; for example, in *Katastrophomena woodlandensis* we have observed different individuals both with and without crenulations in the dorsal valves (Text-fig. 11).

Dorsal internal ridges and septa

In other brachiopod groups, the term 'septum' is used for a substantial internal structure, usually at right angles to the valve floor. Since most strophomenoids have relatively little space between the two valves, the term septum is used for much less substantial structures. Indeed there is no real difference in practice between



TEXT-FIG. 7. Cardinalia of Type D, as seen in *Christiania subquadrata*, based on BB 11931; from the Lenoir Formation of Tennessee; × 12.

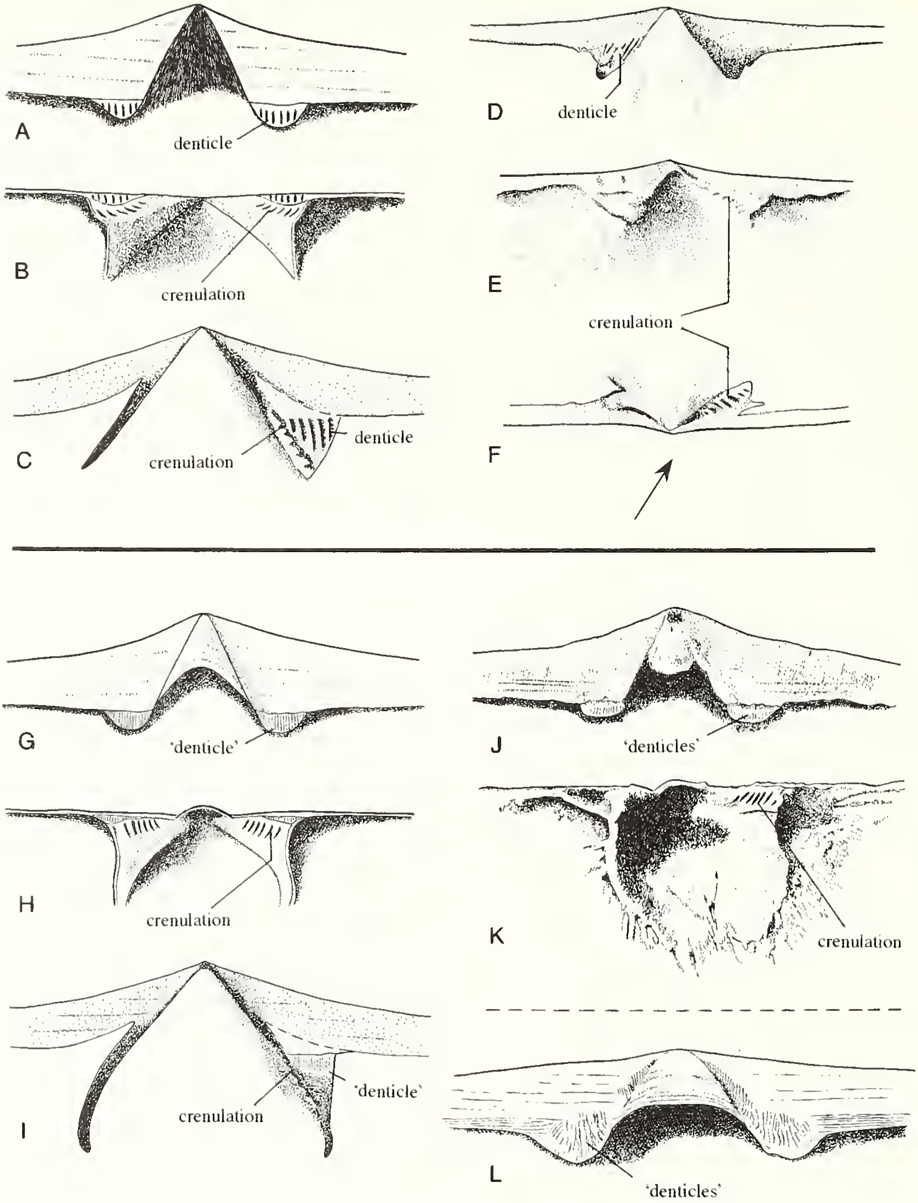
the use of 'septum' and the use of 'ridge', except that the latter can also embrace even smaller structures. We only use the term septum (plural septa) for relatively substantial structures, for example the septa in *Christiania* (Text-fig. 7). There is much variation in septal strength, for example within dorsal valves of *Katastrophomena woodlandensis* the paired side septa can be present or absent in specimens of the same size within the same population and even when present they are of variable strength (Cocks 1968). We use the term 'side septa' in the same way as in the Plectambonitoidea (Cocks and Rong 1989) and include the submedian septa of Williams (1962) and Havlíček (1967), the brachial ridges and brace plates of Harper *et al.* (1967) and Harper and Boucot (1978) and the lateral septa of Zhang (1989). Sometimes the side septa are 1, united with lateral muscle bounding ridges as in *Laevicyphomena*, *Hingganoleptaena* and the 'winglike plates' of *Biparetis* (Text-fig. 3), 2, united with trans-muscle ridges as in *Maakina*, *Oepikina* and *Teratelasma*, and 3, separated from trans-muscle ridges as in *Bekkerina*. The term 'trans-muscle septa' is used for the pair or pairs of septa which diverge anterolaterally as if from a point posteriorly on the median plane of the valve (e.g. in *Oepikina*, Pl. 3, figs 6–7). These trans-muscle septa can also be developed very variably within a single population (Cocks 1968) such as in *Katastrophomena woodlandensis*; however, they are a conservative feature in other stocks.

Other dorsal valve structures

Within the plectambonitoid ancestors of the Strophomenoidea there are two fundamentally different elevated structures with rims running subparallel to the valve margin, the bema and the platform (Cocks and Rong 1989). The bema originates at or near the anterior ends of the socket ridges, whilst the platform originates near to the posterolateral margins of the shell. The bema served as an adductor muscle attachment platform, whilst the raised border of the platform functioned as a barrier to prevent sediment from reaching the lophophore. Some plectambonitoids such as *Leangella* have both bema and platform, although the platform is sometimes developed only in fully mature individuals. The bema is known in strophomenoids (with the possible exception of *Christiania* (Text-fig. 7), but the platform is variably present, even in some of the earliest strophomenoids such as '*Macrocoelia*' *llandeiloensis elongata* of Llanvirn age (Lockley and Williams 1981). The platform is variably developed, usually close to the anterolateral margin of the shell, sometimes in the middle between the bema and the shell margin, and rarely close to the muscle field. In addition there is an internal build-up of secondary shell at the geniculation point of some strophomenoids, particularly *Leptaena*, and we use the term subperipheral rim (= the apophragma of Kelly 1967, p. 591, text-fig. 1). Subperipheral rims can also occur in the ventral valve, but they are relatively uncommon.

Ventral muscle fields and other structures

Dental plates support the teeth and run between the latter and the valve floor. Most strophomenoids possess dental plates, but upon the acquisition of 'strophodontoid' denticles most stocks lack teeth and dental plates, although some early denticulate forms retained them (Williams 1953*a*, fig. 4), and there are sporadic occurrences into the Devonian. The reason for their lack in most 'strophodontoids' is that the strong denticular articulation made their retention unnecessary. There are three basic types of ventral valve interior in strophomenoids lacking hinge line denticles.



TEXT-FIG. 8. The development of denticles. A–F were successful in acquiring denticles and G–L were unsuccessful. A–C, *Eostropheodonta*. A, ventro posterior view of the ventral interarea with open delthyrium and denticulate teeth; B, anterior view of the dental plates with denticles on the top of the teeth and crenulations on the antero-median facets; C, internal mould of ventral valve showing dental plates, denticles and crenulations. D–F, *Eostropheodonta hirnantensis* based on BB 29257. D, internal mould of ventral valve showing dental plates and denticles; E, latex cast of ventral internal mould showing dental plates and crenulations; F, posterior view of ventral internal mould showing dental plates and crenulations: G–I, *Biparetis*. G, ventro posterior view of the ventral interarea with a covered delthyrium and irregular and many finely denticulated teeth; H, anterior view of the dental plates with 'denticles' and crenulations which do not correspond on the antero median facets of the teeth; I, internal mould of ventral valve showing dental plates, irregular and very fine 'denticles' and crenulations. J–K, *Biparetis paucirugosus* based on Oklahoma University 6703; J, ventroposterior view of the

Type A, exemplified by both *Strophomena* and *Leptaena*, has strong teeth and dental plates, and muscle bounding ridges that are usually fused to the anterior ends of the dental plates. These muscle bounding ridges curve round, either to merge anteriorly with the valve floor, or to coalesce anteriorly. There is a wide variety of shape in the muscle bounding ridges, which are sometimes so massive as to be raised well clear of the valve floor. There is often a myophragm (a median ridge between the pairs of muscles) developed, which does not usually start at the valve apex.

Type B, exemplified by *Rainfesquina*, also has dental plates, but these are usually short and straight. Muscle bounding ridges are usually absent or weak, but if they are present are relatively straight antero-lateral extensions of the ends of the dental plates.

The third type has a bilobed muscle field and vascular markings anterior to it, reminiscent of such plectambonitoids as *Leangella* and *Aegiria*. This Type C has a muscle field which is smaller in relation to the entire valve size than Types A and B, and is typified by both *Christiania* and *Foliomena*. Type C can be subdivided into two kinds, C1, with no dental plates, as in *Foliomena*, and C2 sometimes with well-developed dental plates (Williams 1962, pl. 19, fig. 6), although sometimes the dental plates are only visible as stout ridges under the teeth, as in *Christiania* (Cooper 1956, pl. 214, figs 22–24). In C1 there are no bounding ridges, and the muscle field is weakly impressed and usually has a faint border to the field in which a ridge-like myophragm is well developed (Havlíček 1967; Sheehan 1973). In C2, the border of the two diductor scars is often relatively clear since they are bounded laterally by a pair of thin parallel or slightly divergent dental plates. The anterior ends of the two diductor scars are continuous with a pair of vascula media. Six basic patterns of ventral and dorsal muscle fields were recognized by Williams (1953*a*) within the 'strophodontoids'. They are douvillinid, leptostrophiid, megastrophiid, shaleriid, strophodontid, and strophonellid muscle scars. Since the muscle fields of strophodontids and megastrophiids are not fundamentally different, we do not use the term megastrophiid muscle scars. We add the mesodouvillinid type (Text-fig. 9C) as a common shape of muscle scar. There are also (a) some different kinds of bilobate ventral muscle scars (e.g. Text-fig. 9 G–H) and (b) very weak scars without any bounding ridges, as in *Eostropheodonta* (Text-fig. 9A) and *Eopholidostrophia*.

Valve profile and ornament

Since strophomenoid genera were first recognized over a hundred and fifty years ago, one of the main characters used for their separation and identification has been the shape and profile of the valves. For example, *Strophomena* itself is resupinate, and *Leptaena* and *Rafinesquina* are concavo-convex. In addition to overall valve shape, many strophomenoids have a distinctive geniculation, usually dorsally directed, in one or both valves. *Leptaena* is a classic example possessing geniculation (in this case with an interior rim often developed) in both valves. Ventrally-directed geniculation is rare, but occurs in *Altaestrophia*, *Amphistrophiella*, *Kjerulfina*, *Leptodontella*, *Luhaia*, *Odoratus*, *Strophonella*, and *Parastrophonella*. A distinctive bilobed outline is seen in various brachiopod stocks, such as the well-known dalmanelloid *Dicoelosia*, and this is known in the Strophomenoidea only in *Dicoelostrophia*. Ornamentation is very variable; most Strophomenoidea have variations of costellate ornament, but a few genera, such as *Foliomena*, *Laevicyphomena*, *Lissoleptaena*, *Lissostrophia*, and *Pholidostrophia* lack any radial ornamentation. There is some variation in this respect; for example within populations of *Mesopholidostrophia* from the Wenlock Mulde Marl of Gotland, Sweden, most individuals are apparently smooth, but in a small proportion there are faint traces of radial ornament. There are also a few genera which are generally smooth apart from a single median costa, such as *Qianomena* and *Rugoleptaena*. Running across the radial ornament and subparallel to the antero-lateral valve margins there are valve undulations termed rugae. Rugae are developed variably in many strophomenoids, and vary between very regular rugae across the whole valve disc, such as in *Leptaena*, to a minor development near the lateral margins only to be seen in gerontic members of some populations (e.g. the specimen of *Kjaerina typa* figured herein Pl. 3, fig. 2). Sometimes the rugae flow across the radial ornamentation without interruption, but in some genera stronger costellae interrupt the rugae to give a distinctive pattern such as seen in *Bellimurina* and

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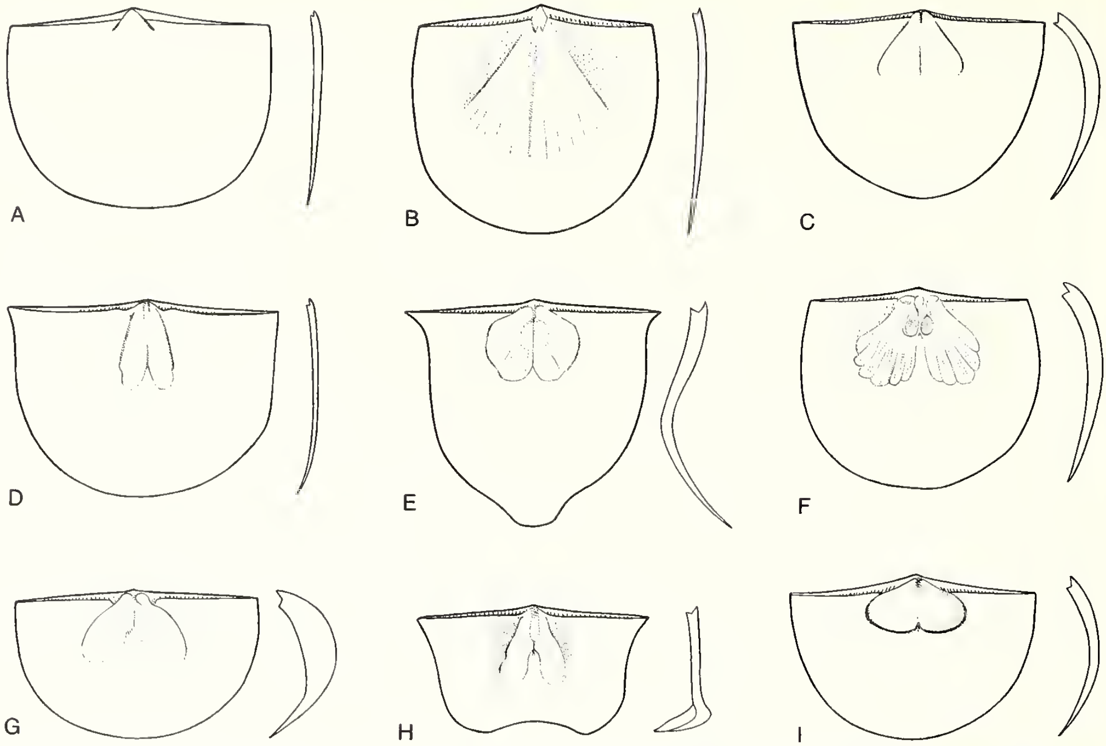
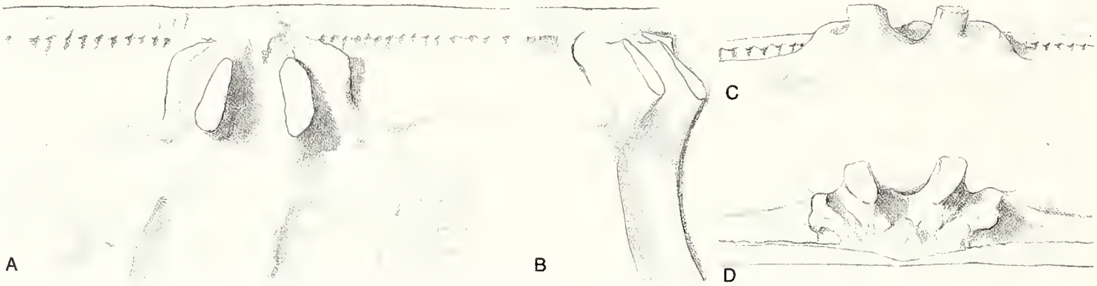
ventral interarea with a covered delthyrium and irregular and finely denticulated teeth; K, anterolateral view of the dental plates with rough and fewer crenulations not corresponding to the 'denticles' on the top of the teeth; L, *Strophomena planumbona*, based on AMNH 30248; ventroposterior view of the ventral interarea with a covered delthyrium and irregular, usually divergent 'denticles' essentially different from those in *Eostropheodonta*.



TEXT-FIG. 9. Ventral valve muscle fields, as seen in internal moulds, and characteristic lateral outlines of various denticulate strophomenoids. A, *Eostropheodonta*; B, leptostrophiid; C, mesodouvillinid; D, shaleriid; E, strophonellid; F, strophodontid; G, *Phragmostrophia*; H, *Leptodontella*; I, douvillinid.



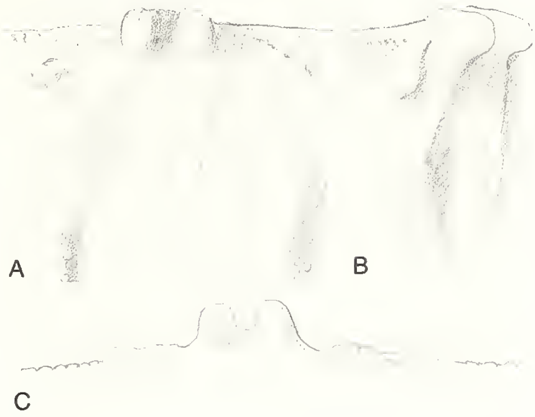
TEXT-FIG. 10. The cardinalia of *Rhytistrophia beckii*, based on AMNH 33167; ×6.

Pentlandinia. Similar patterns are also found in plectambonitoids such as *Ptychoglyptus*. Some of these interrupted rugae form interference patterns, for example the *Limbimurina* figured by Cooper (1956, p. 221, fig. 42).

CLASSIFICATION

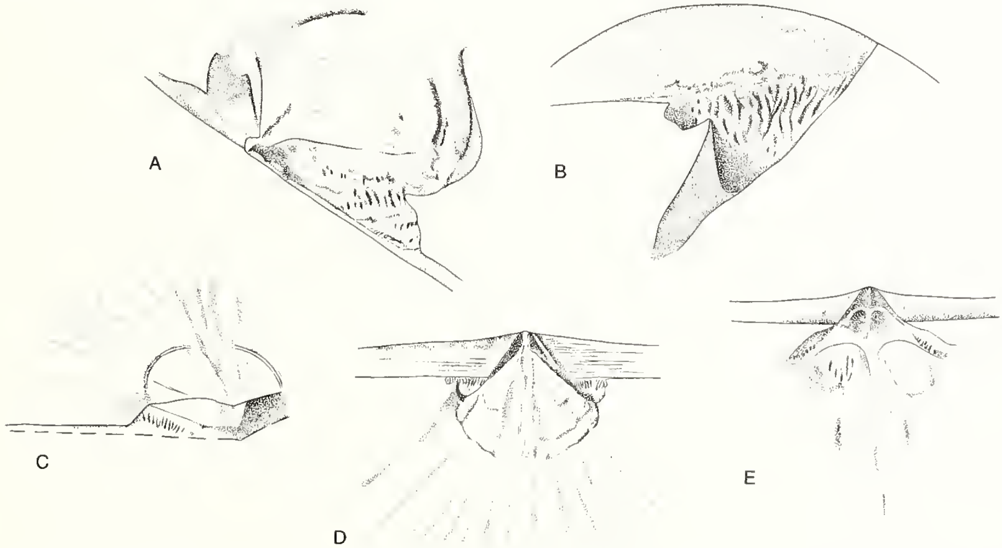
In the past, various workers have used different criteria for allocating strophomenoids to families and subfamilies and for separating and defining genera. However, in the course of our revisions, both of the Plectambonitoidea (Cocks and Rong 1989) and of the Strophomenoidea in the present work, we have become convinced of the prime importance of the position and morphology of the

TEXT-FIG. 11. The cardinalia of *Shaleria* (*Janiomya*) *ornatella*, based on BC 13112; × 12.



cardinalia as the most conservative and fundamental feature to be used in both the discrimination and unification of family rank groups, except within strophomenoids bearing denticulate articulation.

In most published discussions, the diagnoses of families and subfamilies have on analysis proved vague, since too many characters with too much variation have been included. In addition, many structures have neither been described precisely nor evaluated properly, and in some cases a single character has been used by an author to differentiate a new family group with no discussion or appreciation of the effects of using that character in the classification of the whole superfamilial or subordinal group. For example, we have demonstrated in the Plectambonitoidea that resupination can occur in genera related closely to others of normal convexity (Cocks and Rong 1989), but reversed convexity has been used as one of the chief methods of distinguishing two families, the Amphistrophiidae and the Strophonellidae. We try here to develop a supraspecific classification that is based firstly on the evolutionary history of the group, but which is crisply defined and possible



TEXT-FIG. 12. *Katastrophomena woodlandensis*. A–D, Crenulations on the teeth in the ventral valve, E, socket ridges in the dorsal valve. Note the irregular nature of the crenulations, which are homologous to true denticles. A, B, based on BB 66893; A, × 6; B, × 12; C, D, based on B 54506; × 3; E, based on BC 2184; × 3.

for other workers to use. However, we stress that there is great variability within the group, from the population level upwards.

Characters for differentiating families

We follow Cooper (1969 p. 198) in considering that 'the family characters of the genera comprising the family are based on the cardinalia of the dorsal valve and some features of the ventral valve'. Both our experience in many groups of brachiopods have convinced us that Cooper was right; the cardinalia appear to be the most conservative characters in the Orthida and Strophomenida apart from in some denticulate families. We consider that this was probably because of the vitally important function of the cardinalia and also because of the relatively small space between the two valves in the Strophomenida which hindered evolutionary development of the cardinalia which thus became a familial, rather than a generic, character in classification. This is in contrast to the Pentamerida and Rhynchonellida, where the presence of other structures and also the large space between the opposing valves gave more scope for evolutionary changes. It explains why we have been able to identify only three main types of cardinalia in the Plectambonitoidea (simple, trifid or undercut – Cocks and Rong 1989) and four types (described above as A to D) in those Strophomenoida without hinge line denticles. Types A to D form the basis of our definition of the families Christianiidae, Glyptomenidae, Rafinesquinidae and Strophomenidae. However, within those forms with denticulate hinge lines, the separate stocks modified from type B through type E to type F, and in many cases to type G. Thus we cannot separate these denticulate forms on the basis of cardinal process type. One of the bases of familial separations within those forms is the conservative character seen in the shape of the ridges bounding the ventral valve muscle fields (Text-fig. 9) taken with structures such as the median ridge and side septa which are variably developed in the dorsal valve. However, some dorsal internal structures are included in our placing of individual genera within families.

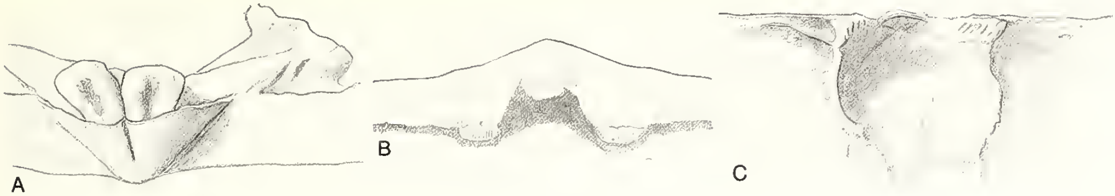
In addition, we recognize as separate families those groups of genera with denticles on the hinge line, as opposed to those which have smooth hinge lines. We do not use the term 'denticulate' for many genera (see Appendix) which have smooth hinge lines, but which have crenulations on the teeth and sockets. However, since we regard the acquisition of denticles as having occurred more than once, we do not group all the denticulate families into a single superfamily – the Stropheodontacea of many authors from Sokolskaya (1960) onwards. Denticulate hinge lines (but with denticles of varying shapes) have been recorded in many different brachiopod stocks, namely the Plectambonitoidea (e.g. *Eoplectodonta*), Chonetidina (e.g. *Eodevoniaria*), Productina (e.g. *Ctenalosia*), which are all Strophomenida, and also in Spiriferida (e.g. *Anthracospirifer increbescens*, *Spiriferinaella* and *Rastelligera*) (Cooper 1969). Only in the 'Stropheodontacea' has this character been elevated to importance in superfamilial diagnosis, which strengthens our rejection of it.

Characters for differentiating genera

Gross changes in valve morphology are recognized here at the generic level, for example resupination and clear geniculation. Occasionally we accept the presence of a substantial fold and sulcus, for example in *Esilia*; however there is much plasticity in this character in some stocks, and it is usually more applicable to differentiation at the specific rather than the generic level. In general, we do not accept variations in the ornament, for example between parvicostellate and fascicostellate, as a valid character for generic differentiation; however, the presence of radial plications and concentric rugae over the whole shell can be of generic importance and the exceptionally distinctive discontinuous costellae seen in *Nervostrophia* is also recognized. Subgeneric status is also according to the lack of finer costellae, as seen for example in *Strophonella* (*Quasistrophonella*). Within the valves the presence or absence of dental plates or socket ridges, muscle bounding ridges, ventral processes, side septa, or substantial diaphragms are used to differentiate genera. However, in the forthcoming *Treatise* volume, we intend to place many genera into synonymy, particularly in the *Leptaena* group, which have been erected on what we consider merely specific or even subspecific criteria.

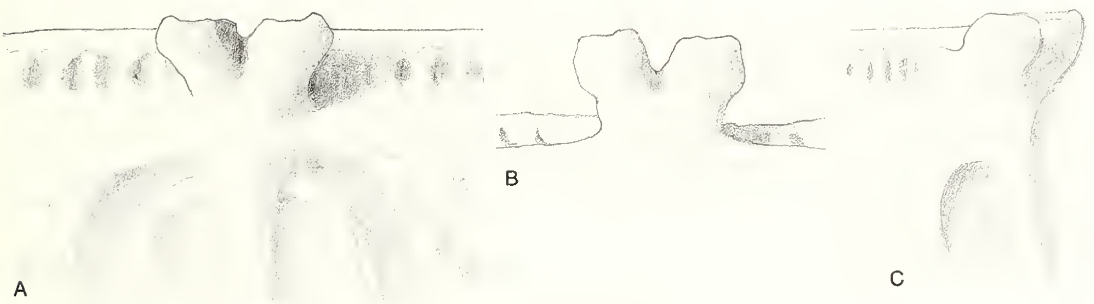
Characters for differentiating species

These vary between genera, but a useful initial concept is that there are seldom more than one species of the same genus in the same bedding plane. Populations of strophomenoids are very often extremely variable, and it is our experience that the greater the number of specimens collected from a single horizon then the less clearcut the differentiation of the species becomes. Thus no further new species should be erected without firstly, a clear knowledge of the internal structures of both valves, and secondly, an appreciation of the



TEXT-FIG. 13. *Biparetis paucirugosus*. A, based on OGS 6716; posterior view of cardinalia showing crenulations on the posterior facets of the socket ridges. B–C, based on OGS 6703; oblique view of ventral valve; B, showing fine 'denticles' on the dorsal facet of the teeth; C, showing crenulations on the posterior part of the anteromedian facets of the teeth. All ×6.

variation present at the type locality. For example, *Eostropheodonta hirnantensis* has both fascicostellate and parvicostellate ribbing in different individuals at the type locality (Temple 1965, p. 411, pl. 17, fig. 6; pl. 18, fig. 7), yet this character has been cited as of familial importance by some authors (e.g. Harper and Boucot 1978, p. 101). The detailed characters for the discrimination of species include details of ornament, relative dimensions of shell shape, and relative proportions of internal structures. However, relative convexity should be used with care; in some populations there is little variability, but in others it is very substantial (e.g. in *Brachiprion arenacea* measured by Cocks 1967, p. 259).



TEXT-FIG. 14. The cardinalia of *Pholidostrophia nacrea*, based on AMNH 37211; ×12.

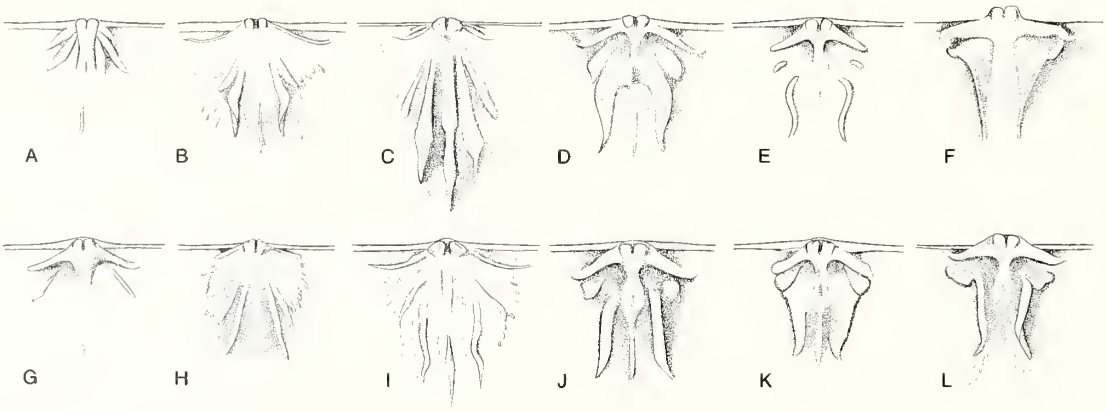
Origin of the strophomenoids

The origin of the strophomenoids is obscure in detail. They are known from several localities in rocks of Llanvirn age: for example, *Trotlandella loki* Neuman *in* Neuman and Bruton (1974, p. 95) from a Whiterock facies block, Holanda, Norway; *Murinella* sp., '*Macrocoelia*' *llandeiloensis elongata* and *Christiania elusa* from the Llanvirn of central Wales (Lockley and Williams 1981); and possibly *Kirkina millardensis* Salmon (1942, p. 599) from the Pogonip Limestone of Utah, USA. There are hitherto no documented strophomenoids from Arenig strata. However, in redescribing the plectambonitoid *Toquimia kirki* from the Antelope Valley Limestone of Llanvirn age from Utah, Ross (1970, p. 64, pl. 8, fig. 17) described a sectioned specimen in which the cardinal process appeared bilobed. This was confirmed by G. A. Cooper (pers. comm.). Bearing in mind that *Toquimia* was assigned to the Leptellinidae because it, like the rest of the family, had a cardinal process that was not undercut, and had no bema or side septa (Cocks and Rong 1989, p. 102), and that those family characteristics are also seen in the earlier strophomenoids, it seems reasonable to postulate that the strophomenoids probably had their ancestors within the Leptellinidae. However, in the Sandaokan Formation of the Ordos Platform, northern part of Shaanxi Province and extending into the southern part of Inner Mongolia, part of the north China plate, an undescribed strophomenoid has been found in Liu Di-yong and Fu Li-pu which is of undoubted Arenig age, since late Arenig conodonts succeeded by early Llanvirn graptolites overly the formation in a structurally uncomplicated section. The specimens are preserved in limestone and the pseudopunctae are clearly visible. The bilobed cardinal process is small and of Type A, the socket ridges are curved posterolaterally and there are weak side septa in the larger specimens, thus this undescribed species is referrable to the Strophomenidae.

THE FAMILIES AND SUBFAMILIES

The Superfamily Strophomenoidea differs from other pseudopunctate brachiopods in its bifid cardinal process (which differentiates it from the Plectambonitoidea) and its lack of spines (which differentiates it from the productoids and chonetoids). Early orthotetoids are impunctate. We include both denticulate and non-denticulate forms within the superfamily. Its included families are as follows.

Family **Strophomenidae** King, 1846. Hinge line non-denticulate. Cardinal process lobes robust, often subcircular (Type A), situated on the posterior part of a well-developed notothyrial platform. Discrete, strong socket ridges often curved round laterally at their ends. The subfamily Strophomeninae King, 1846, has absent or very weak side septa in contrast to the subfamily Furcitellinae Williams, 1965, in which dorsal muscle field bounding ridges and side septa are well developed (Text-fig. 15). Typical strophomenine genera are *Actinomena*, *Dactylogonia*, *Holtedahlina*, *Longvillia*, and *Strophomena*; typical furcitellines are *Biparetis*, *Costistrophomena*, *Cyphomena*, *Furcitella*, *Katastrophomena*, and *Pentlandina*.



TEXT-FIG. 15. Dorsal interiors showing the variation in genera of the Furcitellinae. A, G, *Furcitella*; B, H, *Dactylogonia*; C, I, *Oepikina*; D, J, *Pentlandina*; E, K, *Katastrophomena*; F, *Biparetis*; L, *Quondongia*.

Family **Rafinesquinidae** Schuchert, 1893. Hinge line non-denticulate. Cardinal process lobes usually elongate or plate-like and they remain entirely discrete throughout ontogeny (Type B). Notothyrial platform variably developed. Socket ridges straight, often thinner and smaller than the Strophomenidae. The subfamily Rafinesquininae Schuchert, 1893, lacks geniculations and rugae (except posterolaterally) whilst the subfamily Leptaeninae Hall and Clarke, 1894, is geniculate and usually rugate over most of the shell. Typical rafinesquinine genera are *Hedstroemina*, *Kjaerina*, *Rafinesquina*, and *Rhipidomena*; typical leptaenines are *Hingganoleptaena*, *Kjerulfina*, *Leptaena*, *Lissoleptaena*, and *Rugoleptaena*.

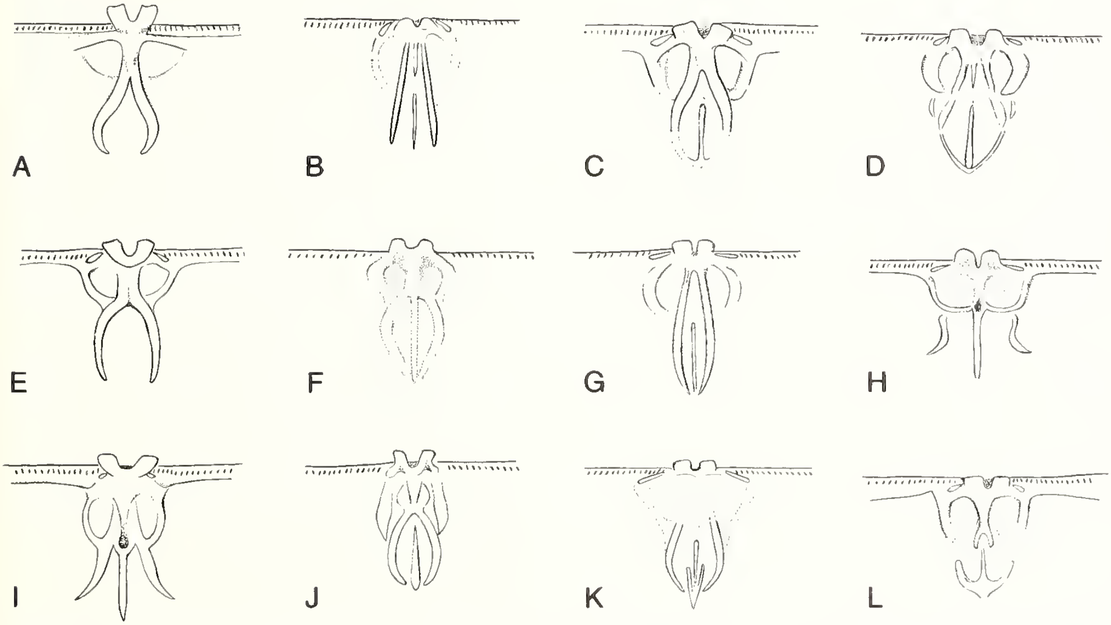
Family **Glyptomenidae** Williams, 1965. Hinge line non-denticulate. Small cardinal process lobes at or largely posterior to the hinge line (Type C). Socket ridges fused directly to the lateral bases of the cardinal process lobes. Notothyrial platform usually absent, and there is often a concave area immediately anterior to the cardinal process lobes. The subfamily Glyptomeninae Williams, 1965, lacks side septa in the dorsal valve and the subfamily Teratelsaminae Pope, 1976, possesses them and a high median dorsal septum. Typical glyptomeninine genera are *Bystromena*, *Glyptomena*, *Paromalomena*, *Platymena*, and *Rhactomena*. The Teratelasminae is monogeneric.

Family **Foliomenidae** Williams, 1965. Hinge line non-denticulate. Cardinal process like the Glyptomenidae (Type C), but family without radial ornament, lacking dental plates, ventral muscle field small and bilobed, and with a pair of close and narrowly divergent side septa. The only firm attributed genus is *Foliomena* (= *Jielingia*).

Family **Christianiidae** Williams, 1953. Hinge line non-denticulate. Low cardinal process with lobes very close together and fused at their bases (Type D). Socket plates often elevated anteriorly from the valve floor. Two pairs of distinctive large septa present in the dorsal valve. Ventral valve muscle field small and bilobed. *Christiania* (= *Christianella*) is the only genus.

Family **Leptaenoideidae** Williams, 1953. Hinge line non-denticulate. Bizarre forms with ventral valve attached to the substrate by cementation. Dorsal interior only known in *Leptaenisca*, which has strong, ventrally-directed cardinal process lobes. Thin low short socket ridges close to the cardinal process. The genera attributed are *Leptaenisca*, *Leptaenoidea*, *Leptaenomendax*, and *Liljevallia*.

Family **Amphistrophiidae** Harper, 1973. Hinge line denticulate. Cardinal process variable. Lacks dental plates. Ventral muscle field semi-elliptical in outline, bounded laterally by curved bounding ridges (except *Eoamphistrophia*). Dorsal muscle field bounded posterolaterally by low ridges extending anteriorly from the socket ridges. No side septa. The subfamily Amphistrophiinae is resupinate and the Mesodouvillininae Harper and Boucot, 1978, is concavo-convex. Typical amphistrophiine genera are *Amphistrophia*, *Devonamphistrophia*, and *Eoamphistrophia*; typical mesodouvillinines are *Maoristrophia*, *Mclearnites*, *Mesodouvillina*, and *Sinostrophia*.



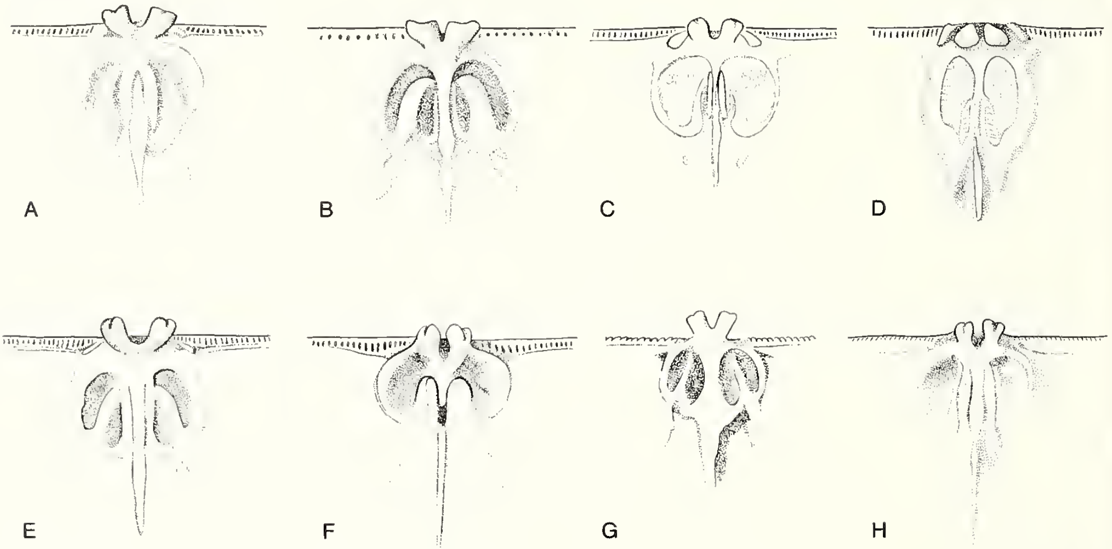
TEXT-FIG. 16. Dorsal interiors of genera of the Protodouvillininae. A, *Protodouvillina*; B, *Douvillinella*; C, *Malurostrophia*; D, *Nadiastrophia*; E, *Douvillina*; F, *Cymostrophia*; G, *Planodouvillina*; H, *Phragmostrophia*; I, *Radiomena*; J, *Telaeoshaleria*; K, *Crinistrophia*; L, *Taemostrophia*.

Family **Douvillinidae** Caster, 1939. Hinge line denticulate. Lacks dental plates (except *Crinistrophia*). Ventral muscle field bilobed and well impressed, usually with bounding ridges laterally and anteriorly. Side septa present. Cardinal process lobes directed ventro-posteriorly and posteriorly. Small socket ridges. The subfamily Douvillininae has an elevated ventral muscle field with overhanging bounding ridges meeting anteriorly; the subfamily Protodouvillininae Harper and Boucot, 1978 (= Douvinellinellinae and Teichostrophiinae, both Harper and Boucot 1978) is like the Douvillininae but without an elevated muscle field; the subfamily Leptodontellinae Williams, 1965, has an elongated muscle field and the widest part of the dorsal valve muscle field occurs anteriorly rather than posteriorly and side septa are poorly developed; and the monogeneric subfamily Dicoelostrophiinae Wang and Rong, 1986, has a sharply indicated, bilobed anterior commissure and two pairs of high septa in the dorsal valve. Typical douvillinines are *Douvillina*, *Douvillinaria*, and

Douvillinoides; typical protodouvillinines are *Cymostrophia*, *Douvillinella*, *Malurostrophia*, *Protodouvillina*, and *Telaeoshaleria*; and typical leptodontellines are *Leptodontella*, *Parastrophonella*, *Sulcatostrophia*, and *Zophostrophia*.

Family **Leptostrophiidae** Caster, 1939. Hinge line denticulate (except *Eostropheodonta*, see above; Text.-fig. 8). Lateral profile biplanate or gently concavo-convex. Triangular ventral muscle field, open anteriorly. Cardinal process lobes usually ventrally directed, but rarely posteriorly. Side septa generally absent. Typical leptostrophiids include *Brachyprion*, *Gibberostrophia*, *Leptostrophia*, *Mesoleptostrophia*, and *Protoleptostrophia*.

Family **Strophodontidae** Caster, 1939. Hinge line denticulate. Subcircular to suboval ventral muscle field strongly impressed, but without bounding ridges anteriorly and often laterally. Dorsal muscle field usually elevated on a platform with bounding ridges. Dorsal median septum and side septa usually, but not always, present. Typical strophodontids include *Galateastrophia*, *Lissostrophia*, *Pholidostrophia*, *Strophodonta*, and *Strophonelloides*.



TEXT-FIG. 17. Dorsal interiors of genera of A–G, the Strophodontinae, and H, Mesodouvillinae showing the origin of the Strophodontinae. A, *Cymbistropheodonta*; B, *Pholidostrophia*; C, *Asturistrophia*; D, *Boucotstrophia*; E, *Strophodonta*; F, *Parapholidostrophia*; G, *Galateastrophia*; H, *Mesodouvillina*.

Family **Eopholidostrophiidae** fam. nov. See below.

Family **Shaleriidae** Williams, 1965. Hinge line denticulate. Parallel-sided and elongate ventral muscle scars with lateral bounding ridges. Dorsal median ridge present which commonly bifurcates anteriorly. Typical shaleriids include *Shaleria* and *Shaleriella*.

Family **Strophonellidae** Caster, 1939. Hinge line denticulate. Ventral muscle field subquadrate and often flabellate, with well developed bounding ridges (except in *Eostrophonella*). Resupinate. Typical strophonellids include *Eostrophonella* and *Strophonella*.

EVOLUTIONARY TRENDS

Like other groups of brachiopod, within most of the Strophomenoidea there are detailed evolutionary trends; however, most described trends have been concerned with denticulate families and genera. Williams (1953*a*) suggested the following 'strophodontoid' trends: (1) the dental plates fusing with the denticular plates and the denticles spreading by increment along the hinge line; (2) the ventral process becoming larger with a corresponding closing of the delthyrium; (3) the socket plates becoming abbreviated; (4) the cardinal process becoming more massive and growing in a posterior direction above the chilidium which became progressively degenerate; and (5) the muscle scars becoming better defined. For the latter, Cocks (1967) described the gradual relative widening of the ventral muscle field in *Brachyprion compressa* from the early Aeronian to the late Telychian. Harper and Boucot (1978) reviewed these trends in detail and also noted an increase in shell size up to the Devonian. These general trends can be recognized as occurring at different rates and in different times within several different and sometimes unrelated stocks. From the taxonomic point of view the two most important trends appear to be the acquisition of denticles, firstly in the cardinal area and subsequently along the entire hinge line, and the change of cardinalia. In this section we also deal with variation in and modifications to the dental plates, pseudodeltidia and the muscle fields of various families within the Strophomenoidea.

Evolutionary trends in the strophomenoids have not been well understood, since there is much variation of many features in some groups and a considerable number of the genera known have not been correctly synonymized. Even though the evolutionary history of the 'strophodontoids' has been far better known than in strophomenoids (Williams 1953*a*; Harper and Boucot 1978) the transformation stages to 'strophodontoids' are still not so clear that it is known whether the 'strophodontoids' are monophyletic or polyphyletic. The original strophomenoid diversification occurred within a short time, with the earliest known representatives of christianiids, glyptomenids, leptaenids, rafinesquinids and strophomenids appearing between the late Arenig and late Llanvirn; in fact the only non-denticulate groups to appear later were the foliomenids and the leptaenoideids. Thus there was an early and rapid differentiation of the critical taxonomic character, the cardinalia, and a great generic diversification during Llandeilo and Caradoc times.

Denticulation

After the differentiation of the cardinalia, some of the Strophomenidae underwent early experimentation in the development of denticulation (Text-fig. 8). There are many Caradoc–Ashgill taxa which bear crenulations and even denticles (see Appendix), and they have the following features: (1) the denticles may be present but are always weak; they may be regular (such as the few denticles in *Dummuckina donax*) or irregular (such as in *Strophomena planumbona*; Text-fig. 3) and can sometimes be very fine (e.g. about fourteen to sixteen microdenticles in *Biparetis paucirugosus*; Text-figs 8, 13); (2) the crenulations are present on the posterior faces of the socket ridges rather than on the posterior margins of the sockets, and are also present on the median-anterior faces of the teeth, usually between two to six in number; (3) the numbers of denticules and crenulations in the ventral valve are often strongly inconsistent; (4) development of the crenulations and denticles is variable, and can be sporadic in the same population; sometimes they are only seen in either the ventral valve or the dorsal valve. Occasionally, a few denticles can be seen in the posterior margin of the sockets (as in *Strophomena filitexta*) and accessory socket ridges with crenulations occur (as in *Oepikina septata*; Pl. 2, fig. 8). During Silurian time, strophomenids declined in both number and diversity. The denticulation in a few strophomenids, such as *Katastrophomena woodlandensis* (Text-fig. 12), still showed the characters of their ancestors. Weakness, irregularity and instability of development of the denticles and crenulations in the Strophomenidae indicate that their adaptive experimentation in this feature was unsuccessful and it can be concluded that no taxon of the family Strophomenidae gave rise to any 'strophodontoids'.

The Leptaeninae is the longest-lived subfamily of the strophomenoids, since it ranged from the Llanvirn to the Carboniferous (Namurian). Many taxa of this subgroup, especially *Leptaena* itself in the Ordovician and Silurian, and even some species of *Leptagonia* in the Carboniferous, also underwent an adaptive experiment in the development of the crenulations and denticles (see Appendix). The crenulations have usually been observed in the dorsal valve where they are located on the posterior facets of the socket ridges, and no crenulations have been found in the posterior margins of the sockets. For instance, in *Mackerrovia lobatus*, from the Telychian of Shropshire, UK, there are about twelve to sixteen irregular and undulate crenulations on the posterior faces of the socket ridges, for example in BC50573. This number of crenulations is more than its Ordovician ancestors, which usually bear two to five crenulations on the posterior faces of the socket ridges. Again, the crenulations can be developed sporadically in the same population. Sometimes the crenulations are quite strong (e.g. Havlíček 1967, pl. 15, fig. 16 for *Leptaena depressa*), but usually they are weak. Thus in the development of true denticulation the *Leptaena* subgroup, like the Strophomenidae, was also unsuccessful and no 'strophodontoids' were derived from the Leptaeninae.

The Glyptomenidae includes only a few taxa with crenulations, perhaps because most of the later representatives of the group (such as *Bystromena* and *Paromalomena*) are small and did not develop crenulations to strengthen their articulation; however, a few earlier and larger taxa, such as *Mjoesina moorei* Mitchell, 1977, do bear crenulations. This group declined in the Silurian, consisting only of *Linostrophomena* and *Qianomena* in South China in the early Aeronian and Telychian (Rong and Yang 1981), which possess no crenulations. Like the Leptaeninae and Strophomenidae, the Glyptomenidae do not seem probable ancestors of the 'strophodontoids'.

The earliest known strophomenoids with crenulations (mainly pits) on the antero-median faces of the teeth and on the posterior faces of the socket ridges are known in rocks of Llanvirn age, for example '*Macrocoelia*' *llandeiloensis elongata*, which is a rafinesquinid. Thus the rafinesquinids were possibly the first family to experiment in the development of denticulation, and this occurred in a very early stage of their evolutionary history. During the first stage of denticular development (mainly from the Llanvirn to the Caradoc) rafinesquinids followed the same pattern as the Strophomenidae, in which denticles are present only in the ventral valve and are usually regular but weak, and are located in the same position as those of the Strophomenidae. There are many taxa with such immature denticulation (Appendix). During this stage, in rafinesquinids and also in strophomenids and glyptomenids, the delthyrium is covered in one of three ways: (1) completely, by a well-developed pseudodeltidium (such as in *Maakina kulinnensis*, *Oepikina*? *walliensis*; *Strophomena planumbona* (Pl. 1, figs 5–6), and *Trigrammaria virve*); (2) partly, by a pseudodeltidium (such as in *Biparetis paucirugosus*, *Furcitella plicata*, '*Macrocoelia*' *stenomuscula* and *Ranfinesquina alternata* (Pl. 2, fig. 7); (3) apically, by a small pseudodeltidium (such as in *Actinomena orta*, *Bellimurina tenuicorrugata*, *Longvillia grandis* and *Mjoesina moorei*). The earliest denticulate forms have an open delthyrium, which may have an apical pseudodeltidium. Therefore, the partial or complete absence of a pseudodeltidium appears to have favoured the acquisition of denticulation.

In the second stage, during late Caradoc and Ashgill times, there occurred some taxa in which the delthyrium was open, with the pseudodeltidium either very small or absent, apart from some forms such as *Eostropheodonta* spp. (= *Aphanomena*, *Eoleptostrophia* and possibly *Hibernodonta*) and *Origostrophia fragilis* (Mitchell, 1977) with a very small apical cover which may have been supported by a faint ventral process. This stage is characterized by a stable development of both crenulations and denticules in the ventral valve, which Williams (1951) called the denticular plates, emerging from beneath the lamellar layer on either side of the delthyrium. Both denticles and crenulations are seen in the ventral valves on the denticular plates and the median anterior part of the teeth. These should have counterparts in the dorsal valve. However, although there are counterpart crenulations on the posterior face of the socket ridge in the dorsal valve, there are no counterpart denticles to those on the ventral valve denticular plate. Moreover, the denticles in the ventral valve denticular plate are regular and relatively strong, although the numbers of the denticles and crenulations on the different faces of the teeth are usually different. More importantly, both denticles and crenulations in the ventral valve are usually stable in the same population. This applies to many species, for example, *Eostropheodonta parvicostellata* from the Hirnantian beds in South China (Rong 1984). From the point of view of speciation, the establishment of denticulation in the whole population is critical in the transformation of the strophomenoids to 'strophodontoids'. *Eostropheodonta* had wide distribution and a variety of other

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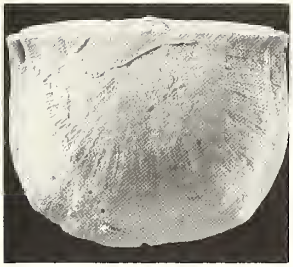
EXPLANATION OF PLATE 1

Figs 1–7, 9–11. *Strophomena planumbona* (Hall); Hudson River Group (late Caradoc); Cincinnati, Ohio, USA. 1–3, 5, AMNH 30247, lectotype; dorsal, ventral, lateral and posterior views of conjoined valves; × 1·5 (except 5, × 2). 4, 6, 10, AMNH 30248; ventral, postero-ventral and enlarged views of ventral interior; 4, × 1·5, 6, × 2, 10, showing crenulations on the teeth; × 6. 7, AMNH 918/5a; dorsal valve interior; × 1·5. 9, AMNH 918/5b; dorsal valve interior; × 1·5. 11, BB 6428; oblique view showing crenulations on the inside of the teeth in the ventral interior; × 8.

Fig. 8. *Strophomena vetusta* James; same locality as above; AMNH 918/5c; enlarged view of cardinal process; × 6.

Fig. 12. *Katastrophomena woodlandensis* (Reed); Woodland Formation (lower Llandovery; Rhuddanian), Woodland Point, south of Girvan, Strathclyde, Scotland; BC 2170; enlargement of natural internal mould of ventral valve to show impression of crenulations on the antero-median face of the teeth; × 10.



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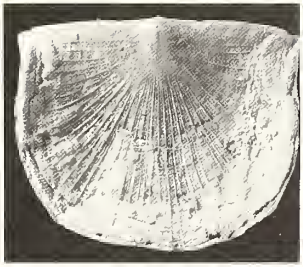

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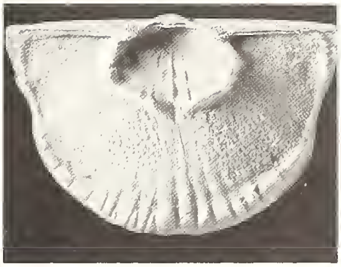

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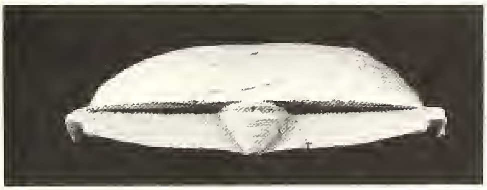

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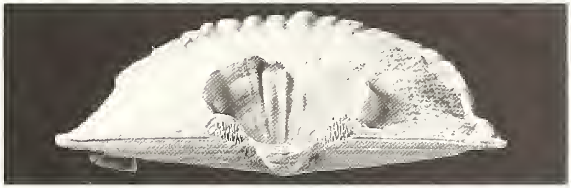

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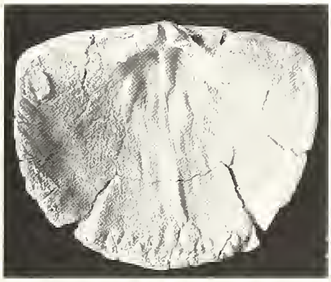

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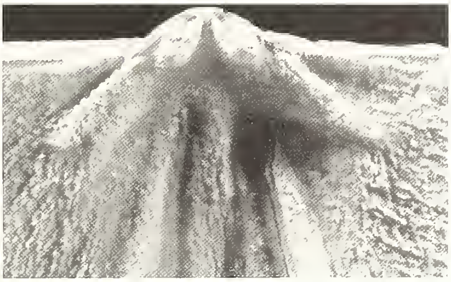

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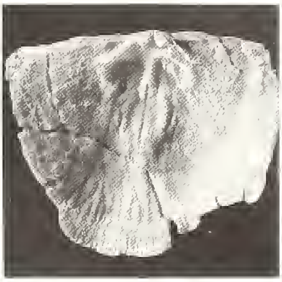

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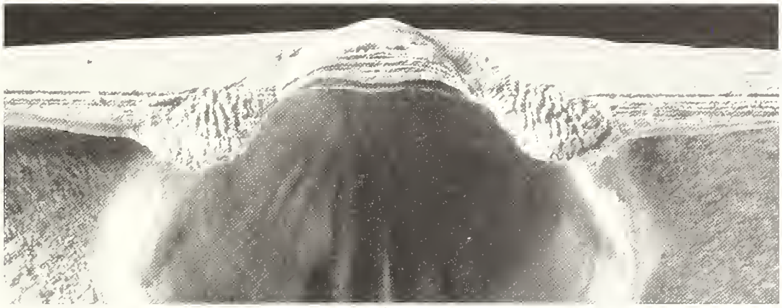

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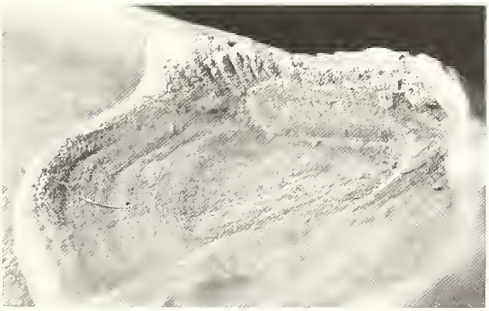

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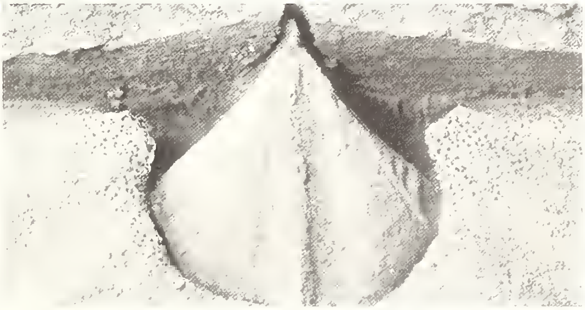

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RONG and COCKS, *Strophomena*, *Katastrophomena* denticulate genera were undoubtedly derived from it by modification of both cardinalia and denticulation, together with other characters. In general, these were relatively flat genera of moderate overall size, a relatively open delthyrium, dental plates and occasionally a weak ventral process. The muscle scars were usually faint. At the beginning of the Llandovery, *Palaeoleptostrophia jamesoni* may have been derived from *Eostropheodonta* by the loss of dental plates, and this became a main stock which later gave rise to many other genera including *Mesoleptostrophia*.

Williams (1953*a*, p. 8) suggested that the earliest known 'strophodontoids' occurred in the Ashgill and Lower Llandovery of Britain. In these forms, there are denticular plates which are fused along their dorsal edges to a pair of short dental plates. We confirm that premature denticular plates (although not true hinge line denticles) occur in many taxa of most groups in strophomenoids in the later Ordovician (see Appendix). The most important development in the origin of the denticulate forms is the development of denticles on the top of the teeth; but to be accepted as such the denticles must be as strong and regular as those in the later stocks, and this is often associated with the loss of dental plates. Before Hirnantian times, there had occurred several taxa of 'strophodontoids' with no dental plates. They are (1) *Origostrophia fragilis* (Mitchell 1977, p. 116, pl. 25, figs 1–13) which possesses thin but very wide denticular plates bearing five to sixteen denticles extending along the hinge line for up to one-half of its width, and possesses a relatively strong ventral process; (2) *Eopholidostrophia portlocki* (Reed) (Mitchell, 1977, p. 114, pl. 26, figs 1–13); and (3) Stropheodontinae gen. et sp. indet. of Mitchell (1977, pl. 25, figs 14–20) which also bear denticles on their teeth. They are all from the lower to middle Ashgill Killey Bridge Formation, Pomeroy, Ireland. In addition, *Eopholidostrophia matutinum* (Lamont) from the Lower Drummuck Group of Girvan, Scotland, also has denticles on the teeth (Harper *et al.* 1967) although Hurst (1974, p. 301) observed that there are no denticles in *E. matutinum* but occasionally the teeth bear extremely fine elongate striations. We have examined the type specimens of *E. matutinum* and confirmed the conclusion made by Harper *et al.* (1967). We consider that the latter situation indicates an initial stage of one 'strophodontoid' stock, i.e. the eopholidostrophiid, a similar developmental trend to that seen in *Eostropheodonta*. But the origin of this stock is still unknown. It is important to note that all the taxa mentioned above with denticles or crenulations in their ventral valves, and with no dental plates, bear no denticles on the hinge line in the dorsal valve (that is, on the posterior margins of the sockets), although the socket plates are crenulated. Thus this is a distinctive feature of the initial stage in the evolution of denticulate Strophomenoidea.

The third stage in the evolution of denticulation was mainly in early and middle Llandovery times, when many taxa evolved which bear denticles in both valves for the first time, although others bear denticles only in the ventral valve and they are absent in the dorsal valve apart from crenulated socket ridges. There are three stocks in which denticles occur in both valves; *Eopholidostrophia sefinensis ellisae*, for example in BB95790, *Eostrophonella eothen* (Text-fig. 5) and *Palaeoleptostrophia jamesoni*, for example in BC2454 (Pl. 6, figs 3–5), all from the Rhuddanian of Britain. However, development of denticles on the posterior margin of the sockets can be present or absent in the same population, indicating an immature developmental stage. The number of denticles and crenulations on the opposite faces of the teeth are nearly the same by this stage in any one individual, and in successive stocks they became identical in number and continuous with each other round the corners of the teeth. In *Eostropheodonta*, the denticles in the dorsal valve are not developed in many species, such as in *E. beechhillensis* (Harper 1973, p. 35), *E. mullochensis* (for example in B73006) and *E. multiradiata* (Temple 1987, p. 81), all Rhuddanian in age, and *E. densa* (Rong and Yang 1981, p. 175) and *E. voraginis* (Cocks 1967, p. 253) from the Aeronian. *Palaeoleptostrophia?* sp. (*Aphanomena* sp. of Harper and Boucot 1978, pl. 1, fig. 2*a–c* from the upper Aeronian of Quebec) has about eight or nine denticles on the posterior margin of the socket; however, no ventral valves are illustrated by Harper and Boucot, and thus the presence or absence of dental plates and the generic attribution is uncertain. Thus the third stage was an intermediate

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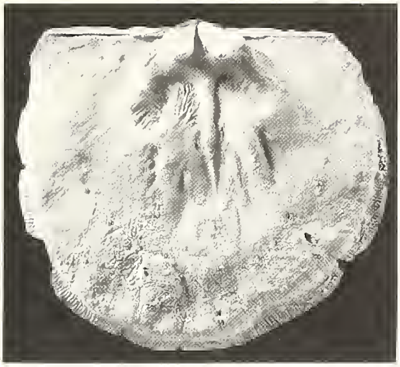
EXPLANATION OF PLATE 2

Figs 1–7. *Rafinesquina alternata* (Hall); Cincinnati Group (upper Caradoc), Cincinnati, Ohio, USA. 1–3, 5–7, B 39912; dorsal interior. 1, dorxal view; × 1. 2, latex cast of dorsal interior, viewed obliquely showing crenulations on the posterolateral facet of the socket plate; × 5. 3, latex cast of dorsal interior, for comparison with material preserved as only internal moulds; × 2. 5–7, anterior, lateral and postero-dorsal views of the cardinalia; × 5. 4, BB 13088; lateral view of the cardinalia of another specimen; × 5.

Fig. 8. *Oepikina septata* Salmon; Lebanon Formation (Caradoc), roadcut on US Highway 41, 14·5 km SE of Murfreesboro, Tennessee, USA; USNM 117829c, holotype; posterior view of dorsal valve; × 8.

PLATE 2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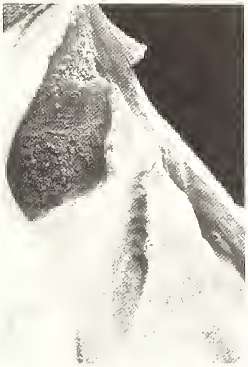
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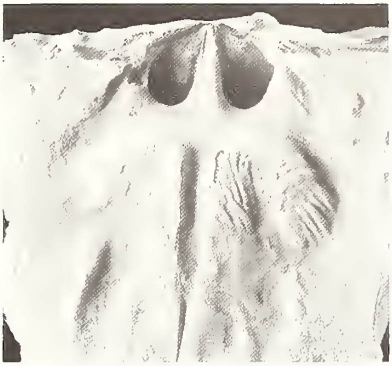
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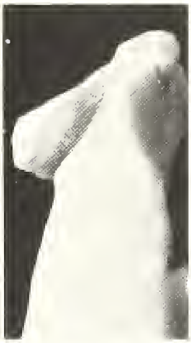
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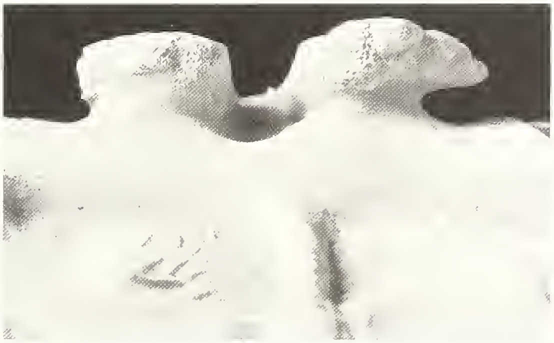
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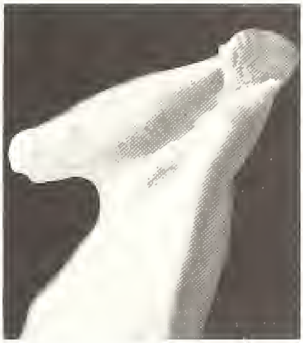
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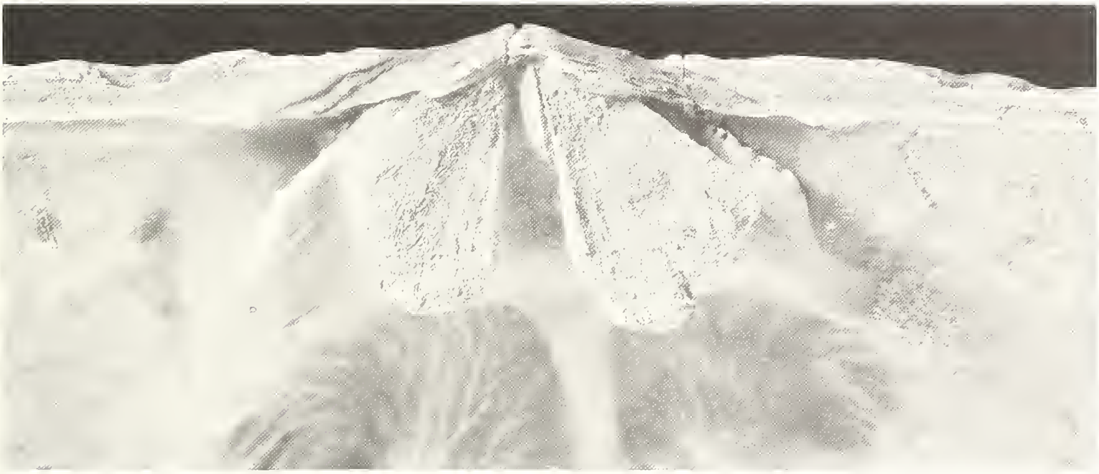
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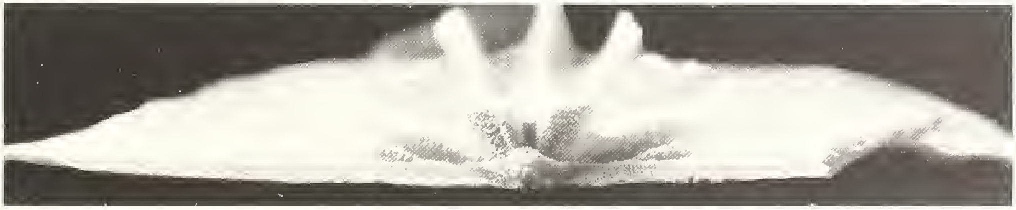
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RONG and COCKS, *Rafinesquina*, *Oepikina* but distinctive stage in which the establishment of denticulation was earlier in *Eopholidostrophia*, *Eostrophonella* and *Palaeoleptostrophia* than in *Eostropheodonta*. Establishment of denticulation is usually associated with the open delthyrium noted above, loss of dental plates (in most genera), a faintly impressed muscle field with no bounding ridges in the ventral valve, and a weakly impressed muscle field lacking any traces of trans-muscle septa in the dorsal valve.

In the fourth stage (mainly in late Aeronian and later time), the establishment of denticulation was completed in which almost all taxa of the denticulate families bear denticles in both ventral and dorsal valves. As time went by, denticular plates became larger in general, with more denticles on them, and the denticles started to spread gradually and progressively along the hinge line. The general trend in evolution of denticulation in the Silurian was that the more denticles present, the younger the age of the taxon in the same stock, assuming that the absolute size was comparable. We do not put any great systematic value on the absolute number of the denticles or on the proportion of the hinge line occupied by them at any time in the history of the stock, since, as suggested by Williams (1953*a*), the increasing denticulation of the hinge line was progressive ontogenetically as well as phylogenetically. In a very small specimen of the Devonian *Strophodonta* sp. which Williams (1953*a*, pl 2, fig. 9) sectioned, only three denticles were present on either side of the delthyrium, leaving an appreciable length of the hinge line free of them; although the hinge line of the adult forms are nearly completely denticulate. However, it is a general evolutionary trend that early forms have fewer denticles in adult stages and later forms numerous denticles. Crenulations on the posterior faces of the socket ridges, when the ridges are present, are conservative structures, which occurred as early as the Llanvirn in strophomenoids and are also present on Silurian forms – for example in *Amphistrophia* (BC4363), *Palaeoleptostrophia* (BC2471) and *Protoshaleria* (BC13112), and in later Devonian forms such as *Megastrophia* (BB16709 Pl. 7, figs 1–2), *Protodouvillina* (AMNH 37217), *Strophodonta* (BB16568), and *Strophonelloides* (B41635; Pl. 6, fig. 9). This may indicate the importance of crenulations in strengthening articulation. In most stocks, the boundary between the third and fourth stages occurred at some time in the Aeronian. Specimens from upper Aeronian rocks (*sedgwickii* Zone) mostly bear well established denticulation although the number of denticles in the dorsal valve may be small. All the ‘strophodontoid’ species we have observed from Telychian rocks possess denticles in the dorsal valve.

The suborder Strophomenidina (including plectambonitoids and strophomenoids) possess deltidiodont rather then the cyrtomatodont hinge teeth which are more efficient in articulation than deltidiodont teeth (Jaanusson 1971). To have the function of keeping the position of the axis of rotation fixed along a long hinge line in strophomenoid evolutionary history, it was necessary to form accessory structures, such as crenulations and denticles, which were developed to fulfil the same function when the teeth became reduced. Thus the denticles functioned as interlocking devices to prevent the valves skewing sideways. Almost no group with cyrtomatodont teeth possesses denticles along the hinge line. The first accessory structures were the crenulations in both the posterior faces of the sockets and the median-anterior part of the teeth in many taxa of strophomenoids (see Appendix). However, all of these stocks were unsuccessful in evolving denticulate hinge lines with the exception of the Rafinesquininae. Stability of the development of denticulation in a population appears to have been the critical factor for the transformation. Denticles first appear on the denticular plates in the ventral valve and subsequently spread laterally along the hinge line. The dorsal valve always acquired denticles later in the history of each stock (Text-fig. 18). This was to achieve a tight interlocking arrangement to maintain the axis of rotation just along the hinge line at all positions of opening or closing the shell, and to avoid transverse and longitudinal movements of the valves relative to each other. The establishment of denticulation, which seems to have been a new advantageous construction, led to a radiation in the Silurian and Devonian. However, although the denticulate families survived the latest Ordovician ice age, they did not escape the Frasnian–Fammenian mass extinction. This was perhaps because either (1) in the early stage of their

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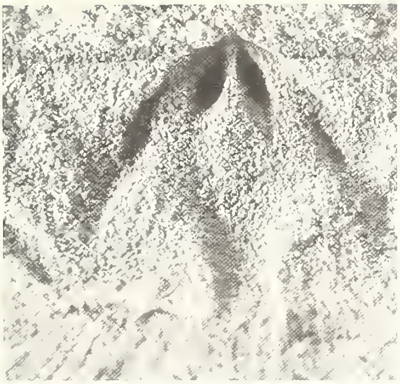
EXPLANATION OF PLATE 3

Figs 1–2. *Kjaerina typa* Bancroft; Cheney Longville Flags (Caradoc: Longvillian), 110 m east of Woolston Quarry, Shropshire, England; BC 13405; natural internal mould and latex cast of dorsal interior; ×8.

Figs 3–5. *Kjaerina bipartita* (Salter); Chatwall Sandstone (Caradoc), Harnage Grange, near Cressage, Shropshire, England; BC 10874; natural internal mould and latex cast of dorsal interior; ×6.

Figs 6–7. *Oepikina septata* Salmon; Lebanon Formation (Caradoc), roadcut on US Highway 41, 14·5 km SE of Murfreesboro, Tennessee, USA; USNM 117829c, holotype; dorsal and anterior views of dorsal interior; ×8.



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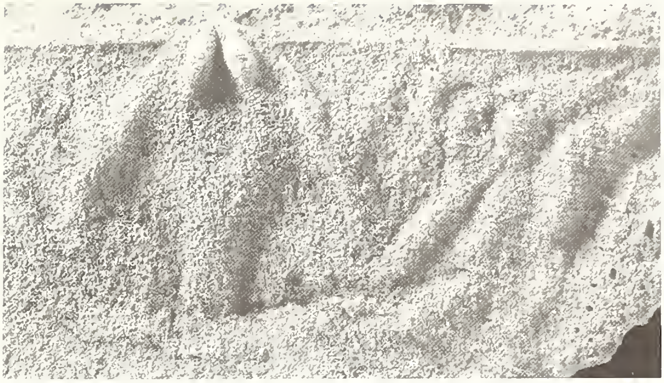

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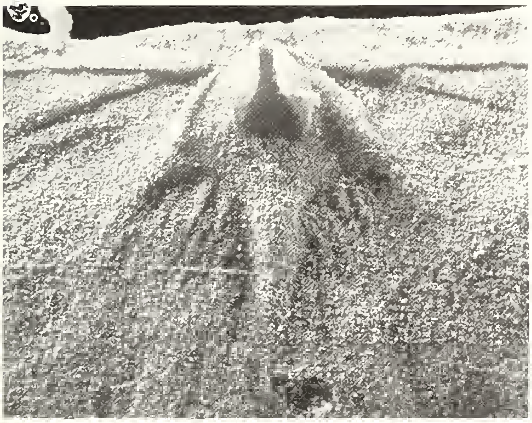

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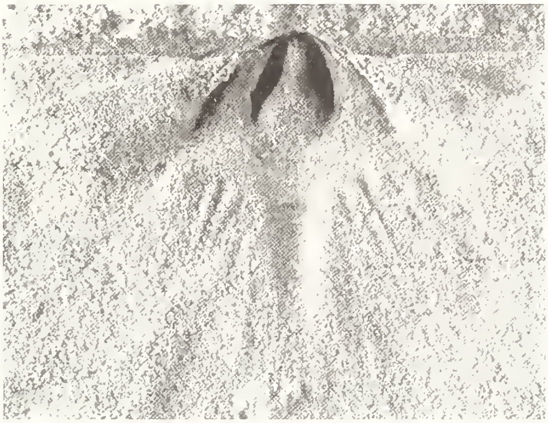

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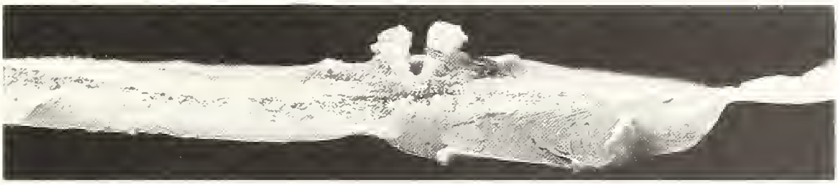

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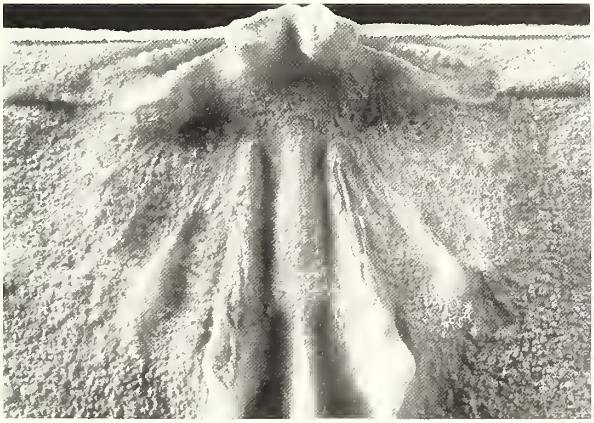

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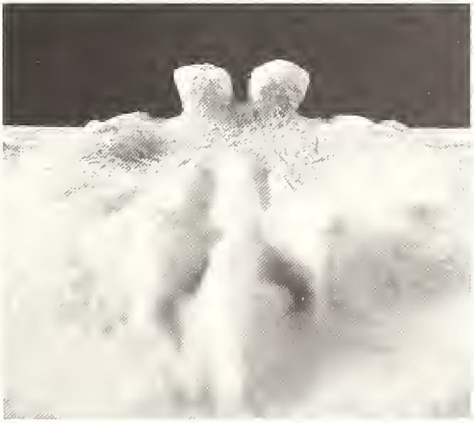

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RONG and COCKS, *Kjaerina*, *Oepikina*

evolutionary history they had great vitality and their novelities, especially the establishment of denticulation, were very favourable to their life habits; or (2) in the later stages of their history they did not adjust to the changing environments and, although they developed existing structures, such as strong forked, posteriorly directed cardinal process lobes there was not enough space for a more developed cardinal process. Thus the 'strophodontoids', like atrypoids and pentameroids, became extinct in the early Fammenian when the ecosystems became impoverished in ecological diversity and in overall species abundance, and it was only their more generalized strophomenoid relatives within the leptaenines which survived into the Carboniferous.

The loss of dental plates in different denticulate stocks also occurred at different times, but occurred mostly before the Wenlock. The earliest known taxa lacking dental plates are *Origostrophia fragilis* and three other species in the lower Ashgill (Mitchell 1977). No taxa lacking dental plates have been recorded from the upper Ashgill and the widespread *Eostropheodonta* bears a pair of dental plates, although these are occasionally vestigial (Rong 1984). At the beginning of the Llandovery, a distinctive genus, *Palaeoleptostrophia* gen. nov. (Pl. 4, fig. 9; Pl. 6, figs 1–5) which was probably derived from *Eostropheodonta*, bears no dental plates and represents a new stock which in turn later gave rise to *Brachyprion* (Pl. 5, fig. 5), *Mesoleptostrophia* (Text-fig. 18) and other genera. Another stock is represented by *Eopholidostrophia* and its close relative *Origostrophia*, which lack dental plates and are known from the Ashgill (*E. portlocki*, *E. matutinum* and *O. fragilis*). *Eomegastrophia* has dental plates but is known from the upper Aeronian (Cocks 1967) and we have found that individuals both with and without dental plates can be seen in the topotype population of *E. ethica* from Shropshire. The earliest *Protomegastrophia*, which lack dental plates, are known from the Telychian, for example *P. prima* and *P. profunda* (Harper and Boucot 1978). The ancestor of *Amphistrophia*, *Eoamphistrophia whittardi*, also lacks dental plates and occurs in the Telychian. All the other denticulate genera in the upper Silurian and Devonian lack dental plates apart from: (1) *Eostropheodonta* sp. which has a pair of very thin, short dental plates and occurs in the Wenlock (Bassett 1971, pl. 56, fig. 7*a*); (2) in a population of *Mesoleptostrophia filosa* from a siltstone overlying the Much Wenlock Limestone Formation a single specimen bears a pair of vestigial dental plates (Bassett 1971, pl 56, fig. 9*a*–*b*); (3) *Pembrostrophia* of Wenlock age possesses variably developed dental plates, but Harper and Boucot (1978, p. 156) regarded them as simply 'the basal part of the denticulate ridges'; (4) *Crinistrophia* and *Papillostrophia* of Emsian age which may have acquired short dental plates secondarily. Therefore the loss of dental plates, which progressed by simple shortening (rather than by a flaring towards, and subsequent merger with, the denticular plates and then the hinge line), may be considered an important trend in 'strophodontoid' evolutionary history (Williams 1953*a*; see also Text-fig. 18).

Cardinalia

The cardinalia of early strophomenoids from Llanvirn to Llandovery times were conservative in the different stocks, hence our reliance on this character for familial classification. However, in later stocks, chiefly the denticulate forms such as the Amphistrophiidae, Strophonellidae and Leptostrophiidae, but also in some stocks with smooth hinge lines such as the Glyptomenidae, Leptaeninae and the Rafinesquininae, the cardinalia evolved as described by Williams (1953*a*). In the earlier denticulate stocks, including *Eostropheodonta*, *Palaeoleptostrophia* and *Eostrophonella*, the cardinal process lobes were bladelike and antero-

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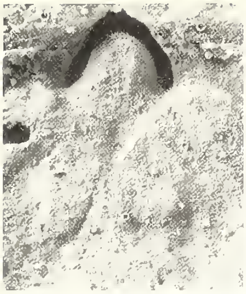
EXPLANATION OF PLATE 4

Figs 1–4. *Leptaena rugosa* Dalman; Dalmanitina Beds (Ashgill: Hirnantian), Ållebergsände, Västergötland, Sweden. 1–2, BB 67944; natural internal mould and latex cast, showing cardinalia of adult specimen; ×5. 3–4, BB 67946; natural internal mould and latex cast of the cardinalia of smaller specimen; ×5.

Figs 5–7. *Longvillia grandis* (J. de C. Sowerby); Marshbrook Beds (Caradoc: Marshbrookian), lane 60 m south of Marshbrook Quarry, Shropshire, England. 5, BB 30638; natural internal mould of dorsal valve; ×1. 6–7, enlargement of the cardinalia of the same specimen and latex cast; ×5.

Fig. 8. *Palaeoleptostrophia jamesoni* (Reed); Woodland Formation (Llandovery: Rhuddanian), Woodland Point, south of Girvan, Strathclyde, Scotland; BC 2471; latex cast of dorsal internal mould; ×8.

Fig. 9. *Rhytistrophia beckii* (Hall); Lower Helderberg Group (Lochkovian), Becraft's Mountain, Hudson, New York State, USA; AMNH 33167, syntype; latex cost of dorsal valve interior; ×6.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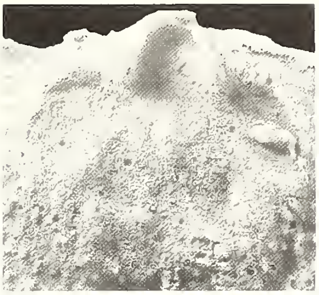
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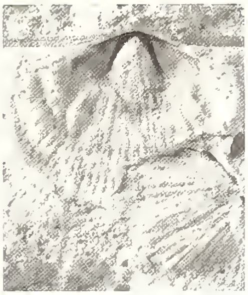
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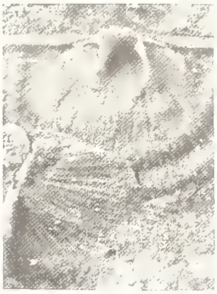
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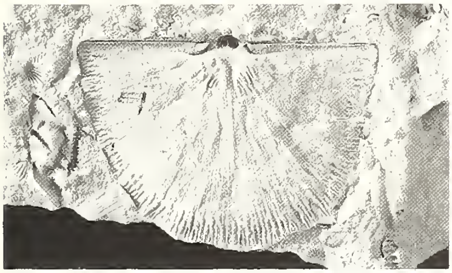
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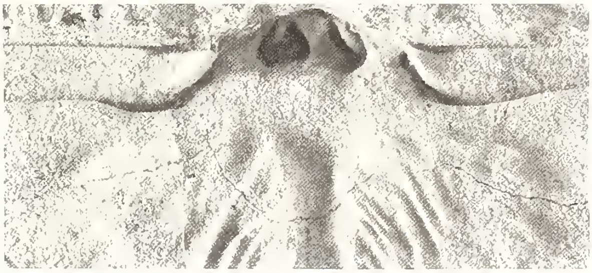
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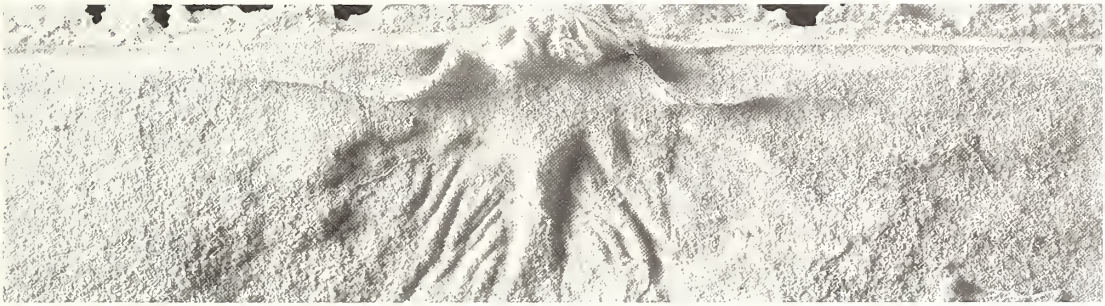
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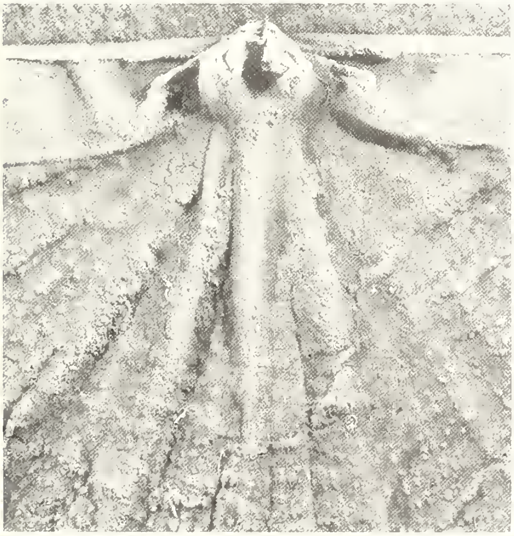
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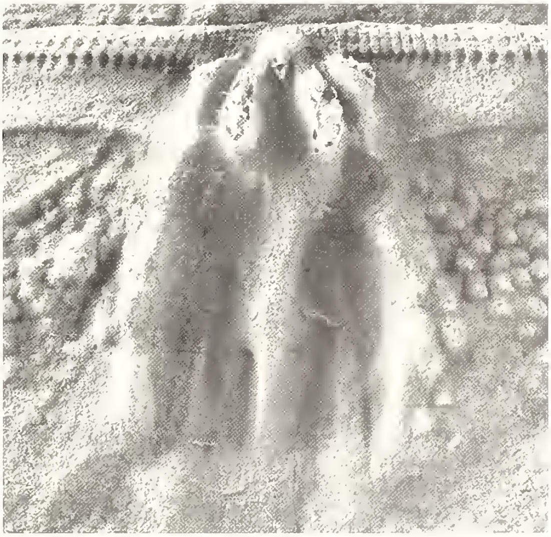
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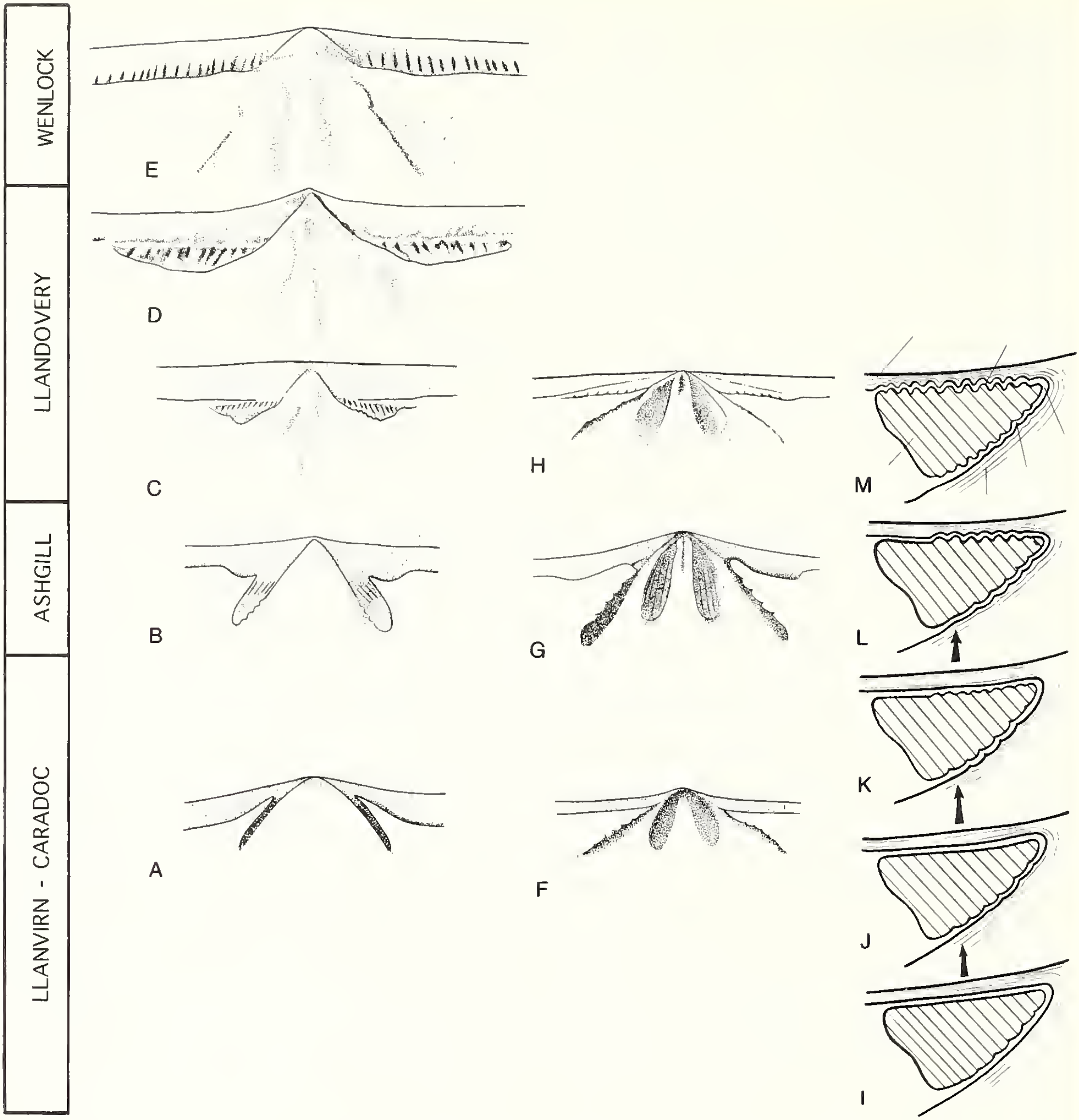
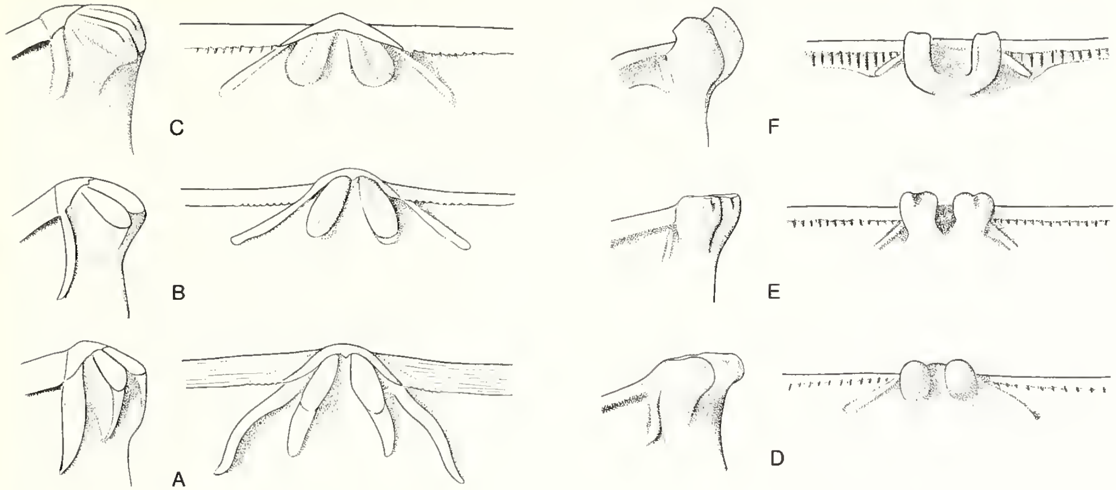
RONG and COCKS, *Leptaena*, *Longvillia*, *Palaeoleptostrophia*, *Rhytistrophia*



TEXT-FIG. 18. Evolution of articulation in the Strophomenoidea in late Ordovician and early Silurian. A–F, internal moulds. A, F, '*Macrocoelia*'; B, G, *Eostropheodonta*; C, H, *Palaeoleptostrophia*; D, *Brachyprion*; E, *Mesoleptostrophia filosa*. I–M, schematic sections through strophomenoidean ventral hinge line, socket ridge and dental plate showing the development first of crenulations and subsequently denticles.

ventrally directed and situated between the pair of socket ridges which were generally stronger and more extensive than the later genera (Text-figs 18–19). The early stage was followed by one in which the cardinal process lobes became shorter and more swollen and progressively more ventrally directed, such as in *Brachyprion*, *Eomegastrophia* and *Protomegastrophia*. The stage is also seen in the late Llandovery leptaenine *Mackerrovia*. However, by middle Llandovery and Wenlock times, the first genera to show the final stage of



TEXT-FIG. 19. The development of cardinalia in the denticulate genera (with the exception of the Leptostrophiidae). A, *Eostrophonella*; B, *Brachyprion*; C, *Amphistrophia*; D, *Shaleria*; E, *Mesodouvillina*; F, *Strophonelloides*. No evolutionary succession from A to F is implied.

evolutionary development had evolved. These include the glyptomenids *Linostrophomena* and *Qianomena* from the middle and upper Llandovery of China respectively, and *Strophonella* (e.g. the well-known *S. euglypha* from the Much Wenlock Limestone Formation), in which the cardinal process lobes are posteroventrally directed (Text-fig. 19).

There is no known case of the reversal of this trend, that is from a posterior facing cardinal lobe ancestor giving rise to an antero-ventral facing descendant. The trend is also known outside the superfamily, within the Orthotetoidea and in some productoids. As the relative size of the cardinal process was also increasing, this was accompanied in many stocks by the spread and effectiveness of denticulation along the hinge line, leading firstly to the loss of dental plates in the ventral valve (see above) and subsequently to the reduction in size (such as in *Leptaenisca*, *Nadiastrophia* and *Sinostrophia*) and even loss of the socket ridges in the dorsal valve (such as in *Lissostrophia*, *Pholidostrophia*, *Protoleptostrophia* and *Rugoleptaena*). The position of the socket ridges also changed to be situated close to the cardinal process lobes. The timing of the change in direction of the cardinal process lobes differs in different stocks, although only a few members of the Leptaeninae and Leptostrophiidae, including *Leptaena* and *Leptostrophia* themselves (Pl. 7, fig. 6), are the only strophomenoids to display ventral-facing cardinal process lobes by Devonian times. Text-figure 20 shows the morphology of the cardinalia of eight genera within the Leptostrophiidae, ranging in age from the late Llandovery to Emsian, in which it can be seen that two separate later stocks evolved from the cardinalia morphology seen in *Mesoleptostrophia filosa*.

SYSTEMATIC NOTES

Genus STROPHOMENA de Blainville, 1824

Strophomena planumbona (Hall, 1847)

Plate 1, figures 1–7, 9–11; Text-figures 3, 8

1847 *Leptaena planumbona* Hall, p. 112, pl. 31B, figs 4*a*–*e*.
1850 *Strophomena* (*Leptaena*) *planumbona* (Hall) King, p. 103.
1892 *Strophomena planumbona* (Hall); Hall and Clarke, p. 249, pl. 9, figs 15–17; pl. 9A, figs 8–9.
non 1956 *Strophomena planumbona* (Hall); Cooper, p. 944, pl. 165, figs 1–2 [= *Strophomena vetusta* James].
1976 *Strophomena planumbona* (Hall); Pope, p. 154, figs 4:3, 5:1–3, 6:2, 7, 10–12.

Lectotype (here selected). AMNH 30247, conjoined valves, J. Hall collection, the original of Hall 1847, pl. 31B, fig. 4*e*, from the Trenton Limestone, Hudson River Group (Caradoc), Cincinnati, Ohio, USA (Pl. 1, figs 1–3, 5).

Discussion. Cocks (1990) reviewed the nomenclature of *Strophomena* and its type species. The genus was erected by de Blainville (1824) in a most peremptory manner, with its only listed species *Strophomena rugosa.* The true identity of *rugosa* has never been satisfactorily established, but there has been an assumption by many authors since the mid-nineteenth century that it is the same as *planumbona.* The position has been regularized finally by the ICZN (1992), which has determined that *planumbona* should be the type species of *Strophomena* and that the binomen *Strophomena rugosa* should be suppressed.

Opportunity is taken here to regularize the concept of *S. planumbona* by selecting a lectotype. Hall (1847, p. 112) mentioned the localities of Cincinnati and Oxford (Ohio), Madison (Indiana) and Maysville (Kentucky) all in 'a position equivalent to that of the Trenton Limestone'. Hall's illustrations of *planumbona* show three external views and one ventral valve interior. The only specimen in the Hall Collection which matches any of these illustrations is AMNH 30247, which has an identical convexity and outline as fig. 4*e*, and which we thus select as lectotype (Pl. 1, figs 1–3, 5). Some confusion also exists as to the true identity of the dorsal valve interior, which Hall (1847) did not illustrate. In the Hall Collection there is a box labelled *Strophomena planumbona* from Oxford, Ohio, in which there are several specimens, which belong to two separate species of *Strophomena.* Following Pope (1976) we determine one type as *S. planumbona* (Pl. 1, figs 7, 9) and the others as *S. vetusta* James (Pl. 1, fig. 8). However, James (1874) did not illustrate his species, and the difference between these two, as well as *S. filitexta* (Hall 1847) and a host of other North American late Ordovician nominal species of *Strophomena*, await further resolution and synonymy, preferably combined with a reappraisal of their relative stratigraphy based on fresh collections.

Genus LEPTAENA and its synonyns

Because *Leptaena*, with its rugosity and geniculation, is such a distinctive genus, a great number of species have been attributed to it since 1828. Many of these species have been promoted to be the types of new genera, but this has usually been done without a survey of related forms, and most workers (including ourselves) have been ignorant of the range of variation to be seen within the *Leptaena* group. Having checked many species assigned correctly to *Leptaena* we have found tremendous variation in shell shape, convexity, ornament, geniculation, the shape of the ventral

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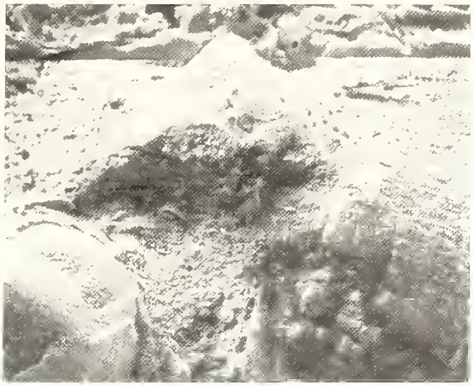
EXPLANATION OF PLATE 5

Figs 1–2. *Brachyprion leda* (Billings); Jupiter Formation (Llandovery: Telychian), 3 km east of Jupiter River, Anticosti Island, Quebec, Canada; GSC 2442, lectotype slab. 1, internal mould of pedicle valve; ×8. 2, brachial valve interior; ×8.

Figs 3–4. *Eostrophonella eothen* Williams; Haverford Mudstone Formation (Llandovery: Rhuddanian), opposite entrance to gasworks, Haverfordwest, Dyfed, Wales; BC 50617. 3, latex cast of dorsal internal mould; ×1·5. 4, enlargement of the cardinalia of a latex cast of the same specimen also showing denticles on the posterior margins of the sockets; ×6.

Fig. 5. *Brachyprion* aff. *compressa* (J. de C. Sowerby); Lower Camregan Grits (Llandovery: Aeronian), Camregan Wood, east of Girvan, Strathclyde, Scotland; B 72901; latex cast of ventral internal mould, showing denticles on denticular plates and not on the hinge line; ×6.

Figs 6–7. *Eopholidostrophia sefinensis* (Williams); Rhydings Formation (Llandovery: Aeronian), Sefin footbridge, Llandovery, Dyfed, Wales; BB 95790; natural internal mould of dorsal valve and latex cast of it; ×4 and ×8.



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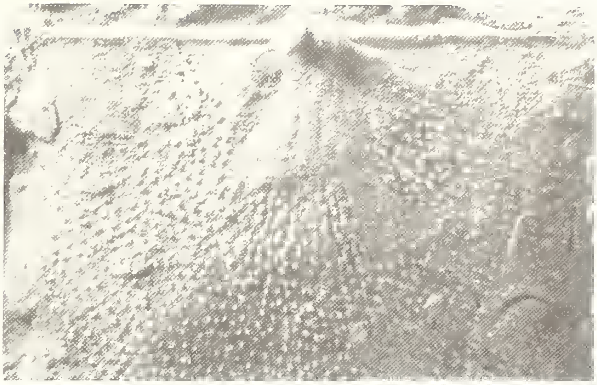

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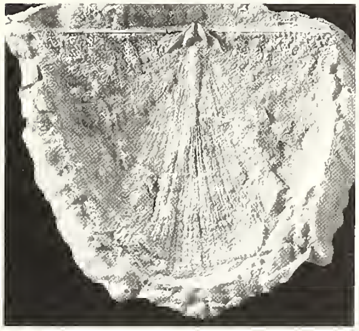

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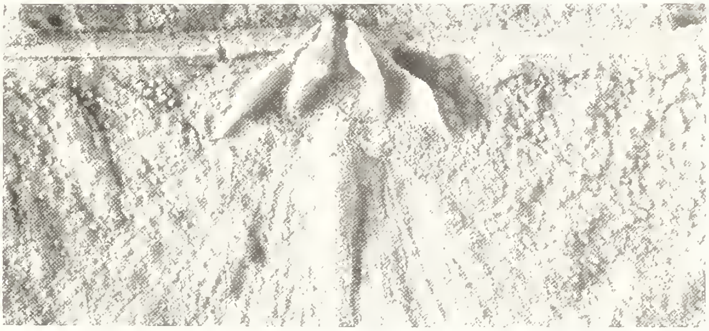

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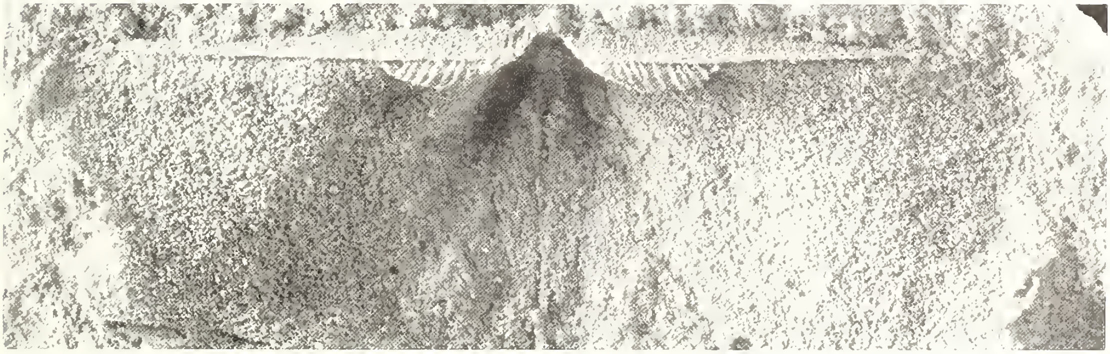

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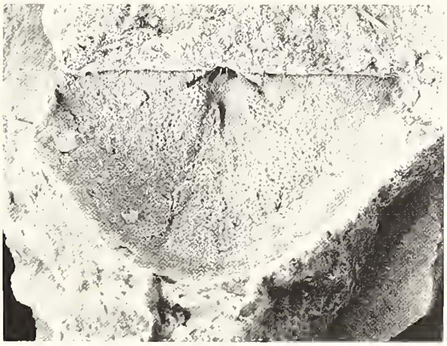

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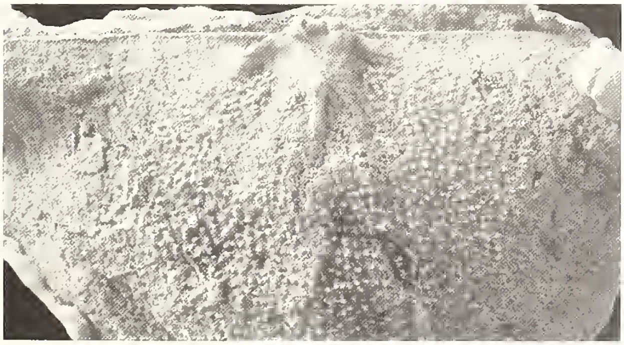

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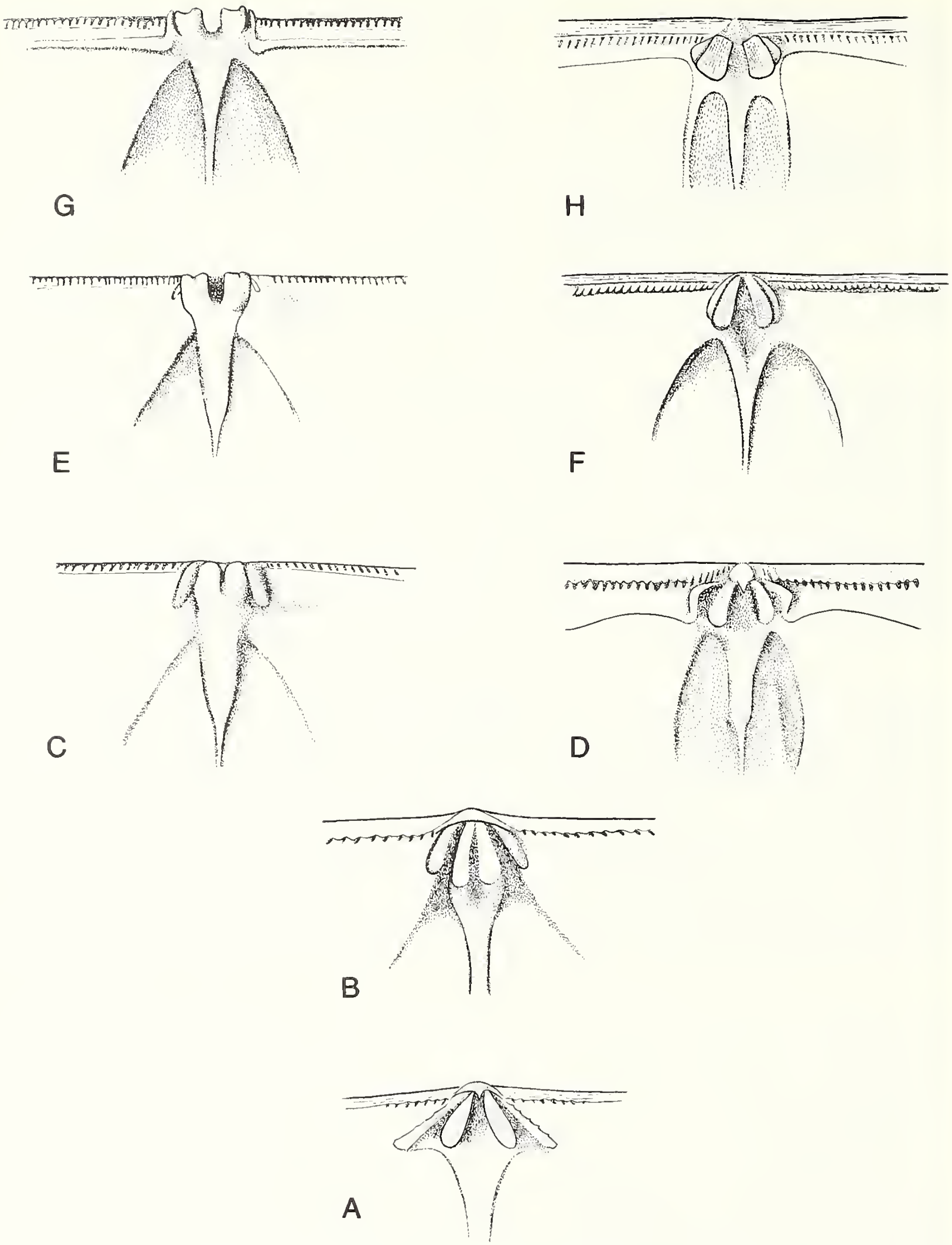
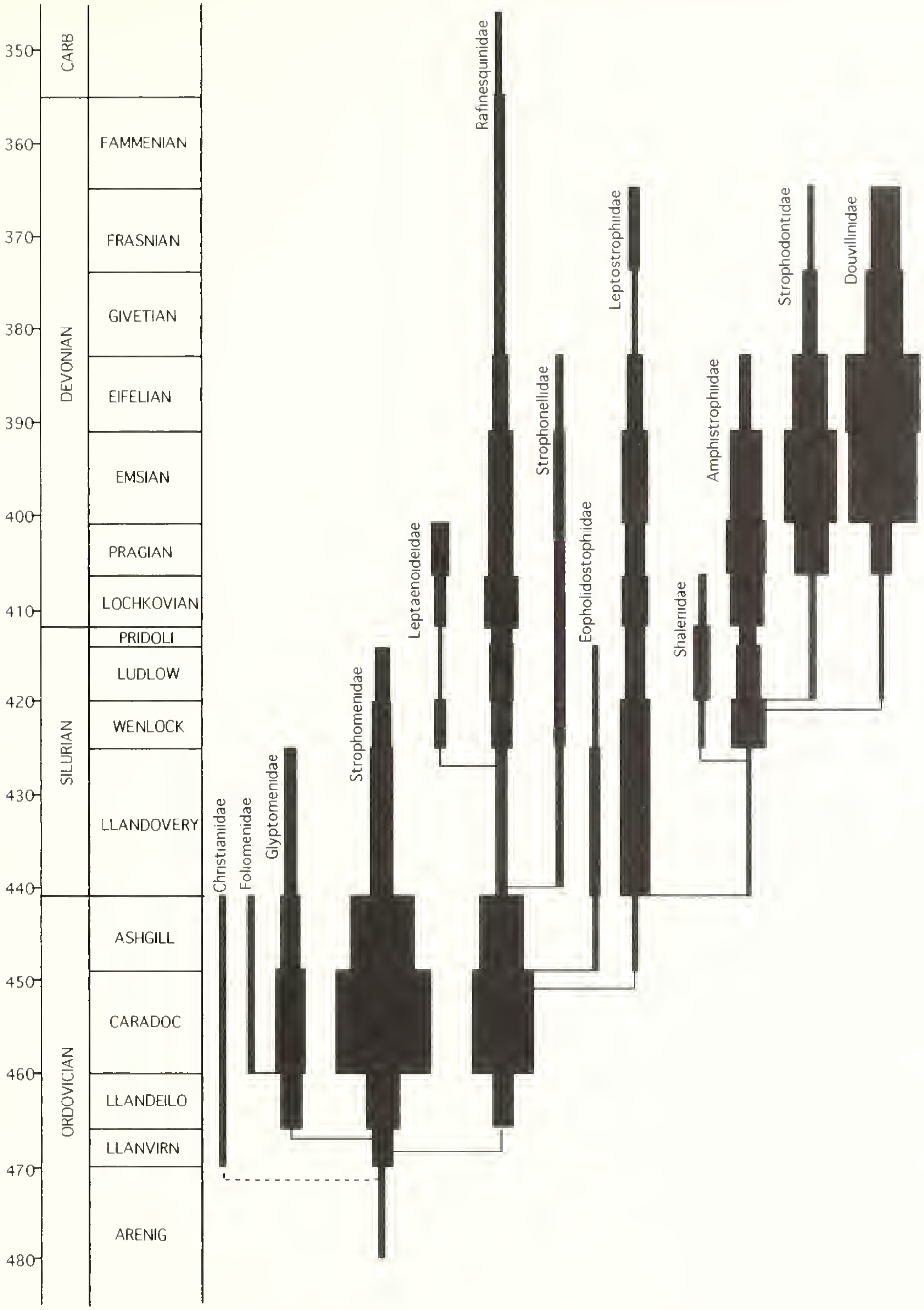
RONG and COCKS, *Brachyprion*, *Eostrophonella*, *Eopholidostrophia*



TEXT-FIG. 20. The development of cardinalia in the Leptostrophiidae. A, *Palaeoleptostrophia jamesoni*; B, *Mesoleptostrophia* (*Mesoleptostrophia*) *filosa*; C, *M.* (*M.*) *kartalensis*; D, *Leptostrophia* (*Rhytistrophia*) *beckii*; E, *Mesoleptostrophia* (*M.*) *explanata*; F, *Leptostrophia* (*Leptostrophia*) *magniventra*; G, *Mesoleptostrophia* (*Paraleptostrophia*) *clarkei*; H, *Leptostrophia* (*L.*) *magnifica*.



TEXT-FIG. 21. The stratigraphical ranges and postulated relationships of the families of the Strophomenoidea. Absolute ages in million years are shown on the left. The widths of the column representing each family indicates relative numbers of genera in each series (in the Ordovician and Silurian) or stage (in the Devonian).

muscle and the diaphragm and the trans-muscle ridges, sometimes within a single population. For example, within a sample of *L. trifidum* from Yichang, China, the trans-muscle ridges vary from absent to faint to reasonably strong (Rong 1984, p. 153). Similarly, the fine median ridge between the cardinal process lobes is variably present or absent in the same sample. These characters form the main basis of the erection of *Leptaenopoma* by Marek and Havlíček (1967) as separate from *Leptaena*, in addition to the 'blade-like brachiophores' present. As can be seen from our topotype *L. rugosa* material (Pl. 4, figs 3–4), the type species of *Leptaena*, the 'brachiophores' (which we term socket ridges) are also blade-like in young specimens, which is why we have placed the two genera in synonymy, following Mitchell (1977, p. 108). In a comparable way, Rõõmusoks (1989) erected seven new genera, apparently based on twelve different characters, but he did not compare them with other genera in the *Leptaena* group (apart from *Similoleptaena*, which he compared only with *Leptaena*). After our analysis we have been able to identify separately only one of his genera (*Septomena*) as a subgenus of *Leptaena* itself, based on the presence of strong trans-muscle ridges which appear to be stable across the population. The others we place into the synonymy of *Leptaena*, apart from *Estonomena* which we consider a synonym of *Kiaeromena*. *Kiaeromena* is itself closely related to *Leptaena*, differing only in its gentle rather than sharp geniculation. The characters which Rõõmusoks used to establish *Astamena*, *Kurnamena*, *Oandumena*, *Schmidtomena* and *Similoleptaena* we regard as being only of specific, rather than generic, importance. Similarly, Havlíček (*in* Havlíček and Štorch 1990) erected *Orhoria* because of the presence of slender socket ridges (which are again like those of young *Leptaena rugosa*, Pl. 4, figs 3–4) and by the lack of a peripheral rim inside the dorsal valve, which is a feature of youth in all leptaenines (the type species of *Orhoria* is small); hence again we synonymize *Orhoria* with *Leptaena*. The type species of *Leptaenella* Fredericks (*L. ventricosa* Hall and Clarke) has been assigned to *Leptaena* by Amsden (1963) for comparable reasons, and we follow him. The monotypic *Turgenostrophia* from the upper Silurian of Mongolia was established by Alekseeva *in* Alekseeva and Erlanger (1983) chiefly based on the absence of a dorsal valve diaphragm, but we consider that character varies substantially within the *Leptaena* group (in addition, her two figured specimens show only ventral valves), and again place the genus in synonymy. *Leptaenulopsis* is founded on small specimens (Williams 1965, p. H391), and the taxon is treated here as a *nomen dubium*.

Thus to summarize, *Astamena*, *Kurnamena*, *Leptaenella*, *Leptaenopoma*, *Oandumena*, *Orhoria*, *Schmidtomena*, *Similoleptaena*, and *Turgenostrophia* are all considered as synonyms of *Leptaena* (*Leptaena*), whilst *Leptaena* (*Septomena*) is considered a separate subgenus, and *Leptaenulopsis* a *nomen dubium*.

Genus BRACHYPRION Shaler, 1865

Brachyprion leda (Billings, 1860)

Plate 5, figures 1–2

1860 *Strophomena leda* Billings, p. 55, figs 2–3.
1865 *Brachyprion leda* (Billings) Shaler, p. 63.
1928 *Brachyprion leda* (Billings); Twenhofel, p. 188 [*pars*] ? pl. 22, figs 10–11.
1978 *Brachyprion* (*Brachyprion*) *leda* (Billings); Harper and Boucot, p. 15, pl. 36, figs 4, 6–7; ? fig. 5.

Lectotype (selected by Twenhofel 1928, p. 188), Geological Survey of Canada GSC 2442 from the Jupiter Formation (Telychian), 3·5 km east of Jupiter River, Anticosti Island, Quebec, Canada.

Discussion. The lectotype is a ventral valve only showing the exterior. It is fortunate, however, that the small slab bearing the lectotype (GSC 2442) includes not only three other ventral valve exteriors but also an excellent dorsal valve clearly showing the cardinalia (Pl. 5, fig. 2), and a ventral interior upon which details of the denticles and denticular plates may be seen (Pl. 5, fig. 1). These specimens resolve some doubts about the genus. In fact *B. leda* is rare within the Jupiter Formation (no specimens were found by one of us in two collecting visits to Anticosti Island) and it seems probable that specimens of *Mesopholidostrophia* had also been included within it by some authors, including Twenhofel (1928). Harper and Boucot (1978) included *Protomegastrophia* and *Eomegastrophia* as subgenera of *Brachyprion*, but we regard the latter as a separate genus, because: (1) the dorsal valve of *Brachyprion* is much less convex than that of *Protomegastrophia* and *Eomegastrophia*; (2) *Brachyprion* has no dental plates and weak muscle bounding ridges within the ventral valve, in contrast to the better developed muscle bounding ridges of *Protomegastrophia* and the presence of dental plates within *Eomegastrophia*; (3) in *Brachyprion* the cardinal process lobes are shorter and less robust than in *Protomegastrophia*, and there is an alveolus present in *Protomegastrophia* which is absent or very poorly developed in *Brachyprion*; and (4) the ventral process is not well developed in *Brachyprion*. Within the dorsal interior of *B. leda* we have seen a small number of faint denticles on the posterior margins of the sockets. The Devonian species, such as *Megastrophia transitans* Johnson, listed under *Brachyprion* by Harper and Boucot (1978, p. 16) have a variety of different brachial valve internal structures – they are all rejected from the genus here.

Other species assigned to Brachyprion

Strophomena anticostiensis Shaler, 1865 (illustrated by Twenhofel 1928, pl. 22, figs 15–18) from the Gun River Formation (Aeronian) of Anticosti Island.

Orthis compressa J. de C. Sowerby, 1839 (revised by Cocks 1967, pl. 37, figs 1–7), from the Aeronian and Telychian of the Welsh Borderland.

Species questionably assigned to Brachyprion

Leptaena waltonii Davidson, 1848 (revised by Bassett 1971, p. 305, pl. 54, figs 1–5), from the Sheinwoodian of the Welsh Borderland (brachial interior unknown).

Strophomena dayi Davidson, 1871 (revised Bassett by 1974, p. 139, pl. 36, figs 11–14), from the Buildwas Formation (Sheinwoodian) of Shropshire (interiors unknown).

Genus PALAEOLEPTOSTROPHIA gen. nov.

Type species. *Strophеodonta jamesoni* Reed, 1917.

Diagnosis. Almost biplanate or very gently concavo-convex. Commonly unequally parvicostellate. Dental plates lacking. Denticles confined to small denticular plates in ventral valve, faint denticles may be present on posterior margins of the sockets in dorsal valve. Cardinal process lobes separated and located between socket ridges (like *Eostropheodonta*).

Discussion. The type species of *Palaeoleptostrophia* was assigned by Harper and Boucot (1978, p. 67) questionably to *Aphanomena* which is considered herein a subjective synonym of *Eostropheodonta* (see below). *Palaeoleptostrophia* resembles *Eostropheodonta* in shell shape, convexity and ornamentation, but it differs from the latter in the absence of dental plates and in the presence of denticles on the posterior margins of the sockets in the dorsal valve. The type species of *Mesoleptostrophia*, *M. kartalensis* from the Emsian of Turkey (Harper and Boucot 1978, p. 68, pl. 3, figs 2–3), is characterized by the distinctive cardinalia in which the cardinal process lobes are close together and converge at their bases on to a median ridge. The socket ridges of *M. kartalensis* are very short and truncated (Text-fig. 20C) and the ventral valve process is well developed, in contrast to *P. jamesoni* in which the ventral process is hardly developed. The well-known late Wenlock to mid-Ludlow species *filosa* was assigned to *Leptostrophiella* by Harper and Boucot

(1978, p. 75), but we regard this species as the earliest representative of *Mesoleptostrophia* (Text-fig. 20B). It is probable that *Palaeoleptostrophia* is the ancestor of *Mesoleptostrophia*, and the point of change is when the denticles migrated on to the hinge line and this coincided with the convergence of the cardinal process lobes on to a median ridge and with the acquisition of the stronger ventral process.

The genus *Castellaroina* occurs in poorly dated, but probably Wenlock or Ludlow age beds in South America. This appears to have a stronger ventral process than *Palaeoleptostrophia*. Examination of the type material of *C. fascifer* (Kayser) reveals that the genus lacks dental plates and is a close relative of both *Brachyprion* and *Palaeoleptostrophia*. It differs from *Brachyprion* in arrangement of the socket ridges and in possessing a stronger and longer cardinal process. *Castellaroina* differs from *Palaeoleptostrophia* in its less well-developed socket ridges and in a stronger and longer cardinal process, and it also possesses a pair of additional enigmatic ridges fused with the hinge line and posterior to the socket ridges.

Palaeoleptostrophia differs from *Brachyprion* in being less convex in its ventral valve, is thinner-shelled, has a stronger notothyrium and thinner but more erect socket ridges, and the anterior parts of its cardinal process lobes converge slightly on to the broad median ridge (Pl. 4, fig. 8). We do not know if *Brachyprion* evolved directly from *Palaeoleptostrophia* or whether the two genera were derived independently from *Eostropheodonta*.

Species assigned

Stropheodonta jamesoni Reed, 1917, from the Rhuddanian of Girvan, Scotland.
Leptostrophia tenuis Williams, 1951, from the Aeronian of the type Llandovery area, Wales.
Leptostrophia ostrina Cocks, 1967, from the Telychian of the Welsh Borderland.

Species possibly assigned

Aphanomena sp. of Harper and Boucot 1978, pl. 1, fig. 2, from the Aeronian of Quebec (ventral valve not known).

Palaeoleptostrophia jamesoni (Reed, 1917)

Plate 4, figure 8; Plate 6, figures 1–5; Text-figures 18, 20, 22

1883 *Strophomena corrugatella* Davidson [*pars*], p. 192, pl. 15, fig. 25; *non* figs 23–24, 26.

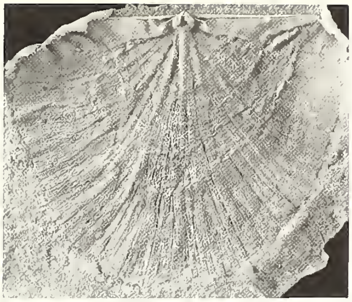
EXPLANATION OF PLATE 6

Figs 1–5. *Palaeoleptostrophia jamesoni* (Reed); Woodland Formation (Llandovery: Rhuddanian), Woodland Point, south of Girvan, Strathclyde, Scotland. 1–2, BC 2471; latex cast and natural internal mould of a dorsal valve; ×1·5. 3–5, BC 2454; natural internal mould of a ventral valve and ventral and anterior enlargements of a latex cast of it showing denticles on denticular plates and on the antero-median parts of the teeth; 3, ×1·5, 4–5, ×8.

Figs 6, 10. *Douvillinaria variabilis* (Calvin); Independence Formation (Frasnian), Middle Amana, Iowa, USA. 6, BB 57970; dorsal interior; ×6. 10, BB 57971; posterior view of conjoined valves showing the narrow and convex deltidium and chilidium; ×8.

Figs 7–9, 11–12. *Strophonelloides reversa* (Hall); Cerro Gordo Member, Hackberry Formation (Frasnian), Rockford, Iowa, USA. 7–9, B 41635; lateral, dorsal and posterior views of a dorsal valve, the latter showing crenulations on the socket ridges; 7–8, ×2, 9, ×6. 11–12, BC 13412; ventral and anterior views of ventral valve, showing the distinctive ventral process; 11, ×2, 12, ×4.

PLATE 6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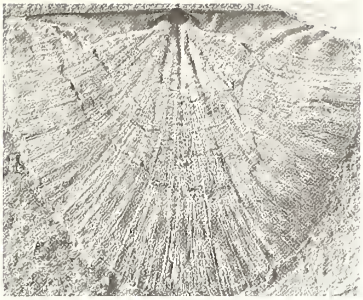
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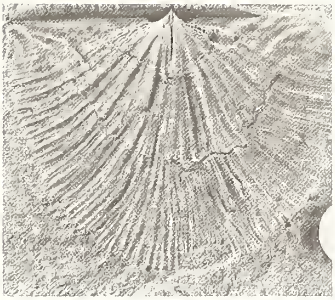
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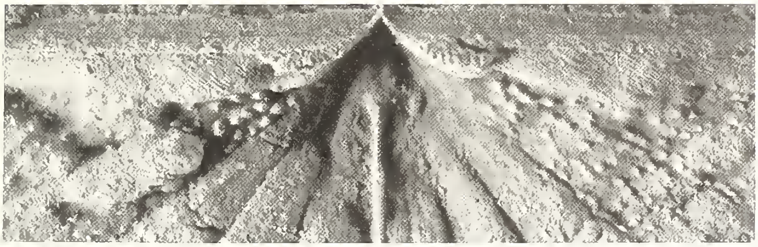
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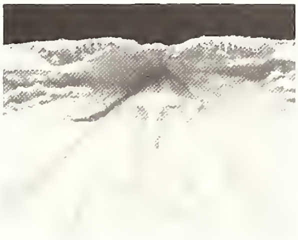
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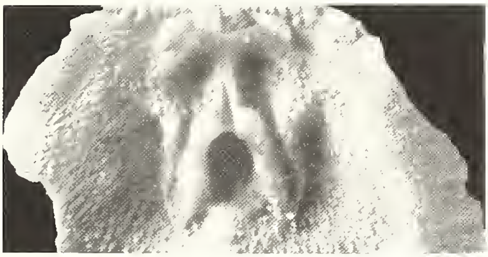
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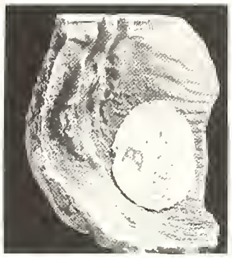
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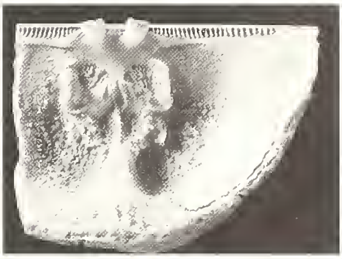
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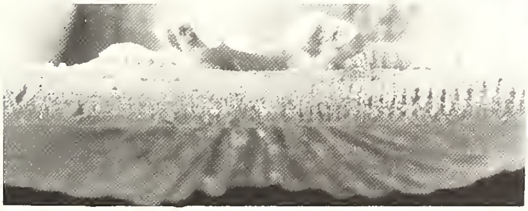
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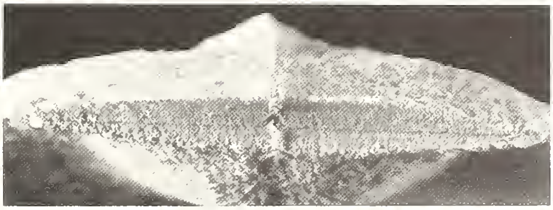
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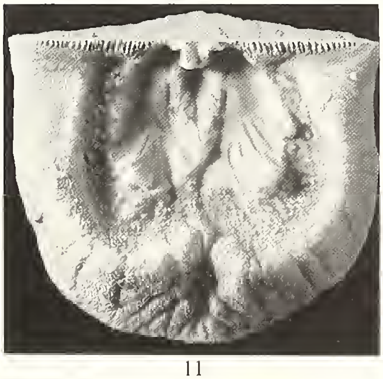
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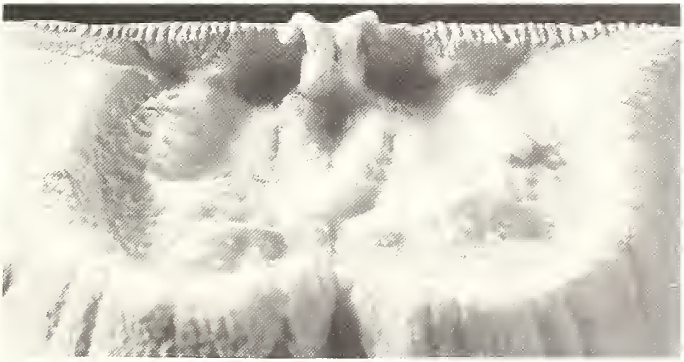
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RONG and COCKS, *Palaeoleptostrophia*, *Douvillinaria*, *Strophonelloides*

1917 *Stropheodonta jamesoni* Reed, p. 893, pl. 16, figs 28–30; pl. 17, figs 1–2.
?1949 *Eostropheodonta reedi* Bancroft, p. 10, pl. 2, fig. 9.
?1951 *Leptostrophia tenuis antecedens* Williams, p. 125, pl. 8, figs 5–6.
1978 *Leptostrophia jamesoni* (Reed) Cocks, p. 127.
?1987 *Leptostrophia antecedens* Williams; Temple, p. 84, pl. 9, figs 10–12.

Lectotype. Selected by Cocks 1978, p. 127, B73036, conjoined valves, the original of Reed 1917, pl. 16, fig. 29, from Woodland Formation (Rhuddanian), Woodland Point, near Girvan, Scotland.

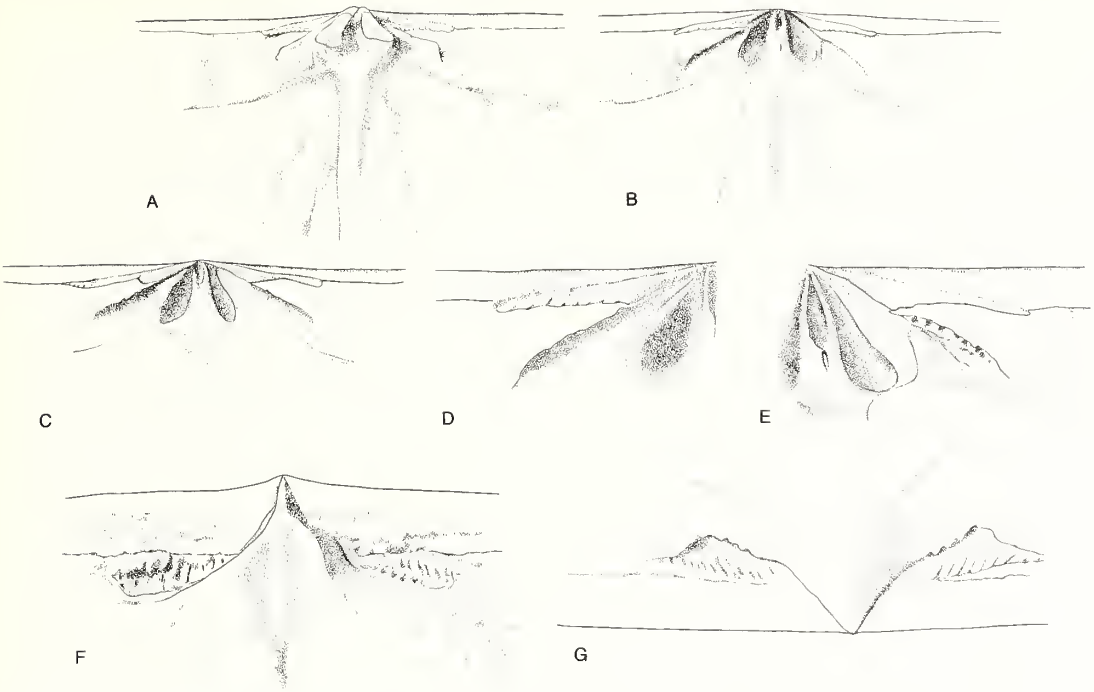
Discussion. Cocks (1978) synonymized *reedi* and *antecedens*, although Temple (1987) preferred to regard *reedi* as a *nomen dubium* and used *antecedens*. Both come from the Haverford Mudstone Formation of Rhuddanian age from Wales. *P. jamesoni* is of the same Ruddanian age and is well represented by more than a hundred specimens in the Gray Collection from the Woodland Formation of Girvan. It is probably a senior synonym of *reedi/antecedens*, but is left in queried synonymy until the Woodland Point fauna is fully revised.

Genus EOSTROPHEODONTA Bancroft, 1949

1949 *Eostropheodonta* Bancroft, p. 9.
1951 *Stropheodonta* (*Eostropheodonta*) Bancroft; Williams, p. 123.
1965 *Eostropheodonta* Bancroft; Temple, p. 410.
1967 *Leptostrophia* (*Eostropheodonta*) Bancroft; Cocks, p. 253.
1967 *Eostropheodonta* Bancroft; Havlíček, p. 81.
1968 *Aphanomena* Bergström, p. 13.
1968 *Leptostrophia* (*Eostropheodonta*) Williams; Bergström, p. 17.
1971 *Leptostrophia* (*Eostropheodonta*) Bancroft; Bassett, p. 318.
1972 *Eoleptostrophia* Boucot *in* Amos, p. 11.
1974 *Rafinesquina*? Hall and Clarke; Amsden, p. 52.
1978 *Eostropheodonta* Bancroft; Cocks, p. 125.
1978 *Eostropheodonta* Lamont; Harper and Boucot, p. 102 [*pars*].
1978 *Aphanomena* Bergström; Harper and Boucot, p. 66 [*pars*].
1984 *Aphanomena* Bergström; Rong, p. 156.
?1985 *Hibernodonta* Harper *et al.*, p. 300.

Discussion. In the upper Ordovician, strophomenoid brachiopods are very common and widespread at many localities, particularly in the uppermost Ashgill *Hirnantia* Fauna. They have attracted the attention of many systematists for more than a hundred years and, as a result, many taxonomic names have been erected for them. As with all other strophomenoids dealt with in this paper, we have looked firstly at the cardinalia, secondly at the presence and positioning of any denticles present, and lastly at other aspects of the morphology such as shape and ornament. The oldest established genus in this group is *Eostropheodonta*, whose type species is *E. hirnantensis* from the uppermost Ashgill of Wales, which was revised comprehensively by Temple (1965). The cardinal process lobes are of Type B, and dental plates are present. There are approximately four to six denticles present on each of a pair of denticular plates; these denticular plates (Williams 1951, p. 122, fig. 22) are the dorsal surface of the teeth, and extend for only a very short distance along the hinge line. On the antero-median facets of the teeth (Text-figs 8, 18) there are also crenulations, which do not usually correspond in number to the denticules. Sometimes an individual denticle continues round the corner of the tooth to be continuous with a crenulation, but this is not always the case. In the dorsal valve there are no denticles on the hinge line (posterior margins of the sockets), but there are crenulations of the posterior faces of the socket ridges which interlock into most, but not all, of the crenulations of the ventral valve.

The ornamentation is variable. In the topotype population of *E. hirnantensis* three types of ornament occur; unequally parvicostellate (Temple 1965, pl. 17, fig. 6), evenly multicostellate (Temple 1965, p. 411) and fascicostellate (Temple 1965, pl. 18, fig. 7), and all variations between these combinations may be found in the Natural History Museum collections. Later authors have



TEXT-FIG. 22. The articulation and cardinalia of *Palaeoleptostrophia jamesoni*. A–B, D–E, BC 2471; dorsal internal mould and latex cast showing denticles on the posterior margin of the sockets and on the anterior facets of the socket ridges, ×6 and ×12 respectively; C, BC 2472; a natural internal mould; ×6; F–G, BC 2454; ventral valve; showing denticules on the denticular plates and viewed ventrally and posteriorly, all from the topotype population from the Woodland Formation (Llandovery: Rhuddanian) at Woodland Point, Girvan, Scotland; ×12.

unfortunately placed undue significance on aspects of the ribbing, for example in Harper and Boucot (1978, p. 101) in the redefinition of the Eostropheodontidae. When Bergström (1968, p. 13) established *Aphanomena* he did not compare it with *Eostropheodonta*, and Harper and Boucot (1978, p. 66) separated the two genera only by the allegedly different ornamentation (parvicostellate in *Aphanomena*, and fascicostellate in *Eostropheodonta*). Boucot *in* Amos (1972) established *Eoleptostrophia* with type species *E. mullochensis*, on the basis of its 'evenly parvicostellate' ornament; after examination of extensive topotype collections, we also assign this species to *Eostropheodonta*.

We have re-examined the type specimens of *Hibernodonta praeco*, BC9195–7, which was established by Harper *et al.* (1985, p. 301), who described the 'hinge line denticulate along at least three-quarters of width'. On the contrary, there are no denticles on the hinge line, although in the ventral valve there are some very weak and poorly defined low denticles on the denticular plates. There are, however, six or seven much stronger crenulations on the antero-median facets of the teeth, and corresponding crenulations on the posterior faces of the socket ridges in the dorsal valve. Thus we consider *Hibernodonta* to be within the generic concept of *Eostropheodonta*, but retain it as a separate subgenus from *E.* (*Eostropheodonta*) because the denticles on the denticular plates are scarcely developed. The age of *Hibernodonta* and the Clashford House Formation in which it occurs is not established definitively, but it has been provisionally assigned to the late Caradoc (Harper *et al.* 1985, p. 289), and thus provides an interesting link between *Eostropheodonta* and its rafinesquinid ancestors. The cardinalia of *Hibernodonta* are very similar to *Hedstroemina*, in which crenulations are found, and also to *Kjaerina* (Pl. 3, figs 1–5), although we have seen no crenulations in the latter genus. We also assign *Brachyprion stropheodontoides* Savage to *Eostropheodonta*. Amsden (1974, p. 52) revised this species and assigned it to *Rafinesquina*?, but he illustrated denticles on denticular plates (1974, pl. 12, fig. 2*i*), which are distributed in the same way as in *Eostropheodonta hirnantensis*. Thus the distribution of the genus ranges from upper Caradoc to lower Wenlock (the *Leptostrophia* (*Eostropheodonta*) sp. of Bassett 1971, pl. 56, figs 7–8) and it occurs over most of the world, with its acme in the *Hirnantia* Fauna of the upper Ashgill.

Genera BOUCOTSTROPHIA, LEPTOSTROPHIELLA, MESOLEPTOSTROPHIA *and* RHENOSTROPHIA

In 1960, Boucot erected *Rhenostrophia* with *Orthis subarachnoidea* d'Archiac and Verneuil as type species. As Jahnke (1971, p. 59) pointed out, there is only one type specimen of *R. subarachnoidea*, which is merely the exterior of a ventral valve, and the genus is therefore best considered as a *nomen dubium* until the type species is properly redescribed from new topotype collections. Jahnke (1971, p. 59) also pointed out that *subarachnoidea* might be conspecific with *Orthis explanata* Sowerby, which is the type species of *Leptostrophiella* Harper and Boucot (1978, p. 74). García-Alcade (1992, p. 66) accepted Jahnke's conclusion, but unfortunately suggested rejection of *Rhenostrophia* in favour of *Leptostrophiella*, which is not allowable under the ICZN rules of priority. After revision, we consider that *Leptostrophiella* is a subjective synonym of *Mesoleptostrophia* Harper and Boucot (1978, p. 68), whose type species, *M. kartalensis* Harper and Boucot comes from the Emsian of Turkey. A further genus, *Boucotstrophia* Jahnke (1981, p. 150), whose type species (*Stropheodonta herculea* Drevermann from the Pragian of Germany) was assigned to *Rhenostrophia* by Harper and Boucot (1978, p. 173).

Since *R. subarachnoidea* has not yet been revised, we are faced with a dilemma. There are at least two separate forms which are firstly, a leptostrophiid, which includes the species *explanata* and *kartalensis*, and secondly, a strophodontid, which includes the species *herculea*. We propose to use *Mesoleptostrophia* for the first form and *Boucotstrophia* for the second form, and treat *subarachnoidea* and its associated genus *Rhenostrophia* as a *nomen dubium*. If *Rhenostrophia* is ever revised and resurrected, then it will probably be a senior synonym of *Mesoleptostrophia*, or less probably *Boucotstrophia*, but we recommend its non-usage.

Family PHOLIDOSTROPHIIDAE Stainbrook, 1943

Stanbrook (1943) erected the subfamily Pholidostrophiinae because of a perceived link between the strophodontids and chonetoids. This was not at first followed by Williams (1953*a*, 1953*b*), who included the group within the Strophoedontinae; but Williams (1965) later defined the subfamily to include *Pholidostrophia* (and its subgenus *Mesopholidostrophia*) and *Lissostrophia* (with its subgenus

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EXPLANATION OF PLATE 7

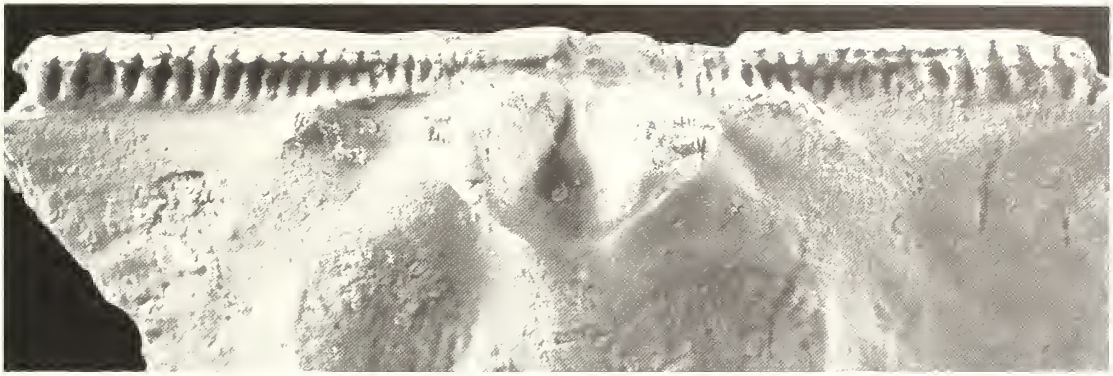
Figs 1–3. *Megastrophia concava* (Hall); Silica Shales, Traverse Group (Eifelian–Givetian), Sylvania, Ohio, USA; BB 16709; postero-ventral, posterior and ventral views of ventral valve showing crenulations on the socket ridges; 1–2, ×6, 3, ×2.

Fig. 4. *Protodouvillina inaequistriata* (Conrad); Hamilton Group (Eifelian–Givetian), Bristol and Canandagua Lake, New York State, USA; AMNH 37217; enlargement of the posterior part of the dorsal interior; ×6.

Fig. 5. *Strophodonta demissa* (Conrad); Upper Ferron Point Formation (Givetian), Alpena, Michigan, USA; BB 16568; enlargement of the cardinalia; ×6.

Fig. 6. *Leptostrophia magnifica* (Hall); Oriskany Sandstone (Pragian), Schoharie, New York State, USA; BC 13063; postero-dorsal view of latex cast of cardinalia; ×3.

Fig. 7. *Amphistrophia* (*Amphistrophiella*) *funiculata* (M'Coy); Mulde Marl (Wenlock; Homerian), Däpps, Gotland, Sweden; BC 4363; enlargement of cardinialia; ×6.



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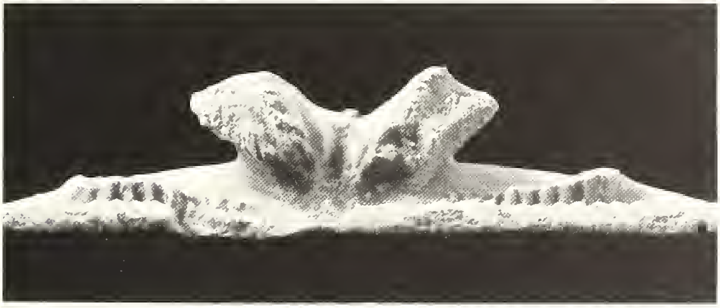

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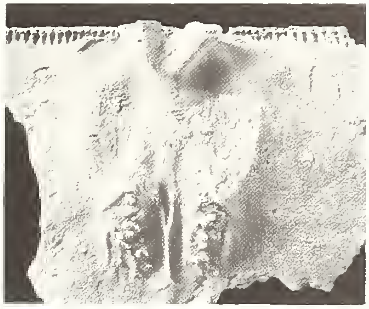

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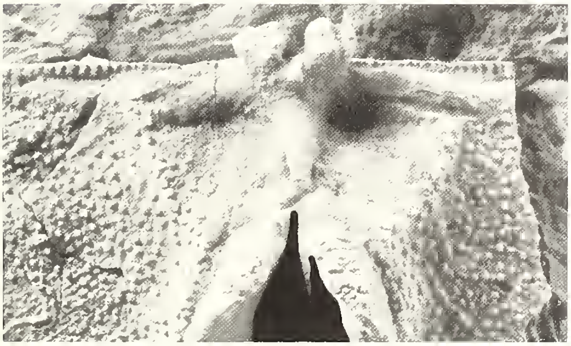

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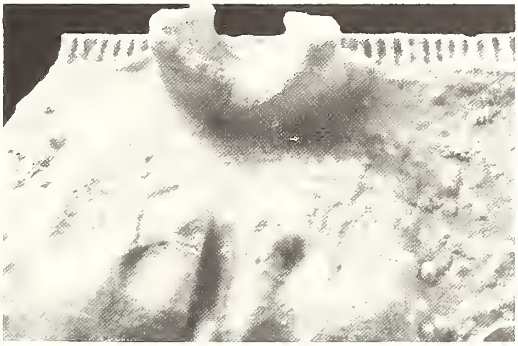

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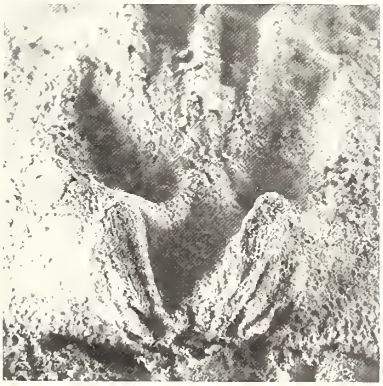

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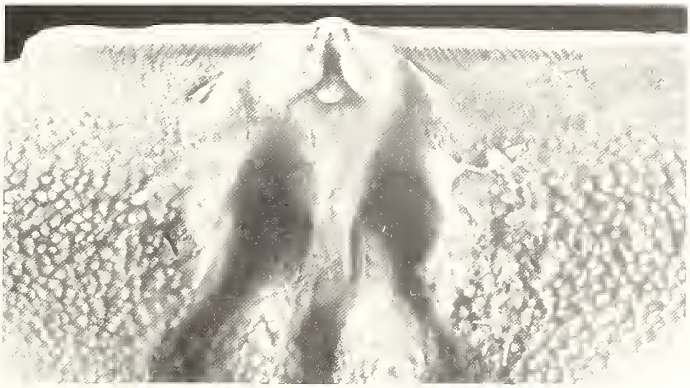

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RONG and COCKS, strophomenoid brachiopods

Mesolissostrophia). Sokolskaya (1960, p. 215) elevated the subfamily to familial rank. A substantial contribution by Harper *et al.* (1967) followed, in which the subfamily included *Ancylostrophia*, *Eopholidostrophia*, *Nadiastrophia*, *Pholidostrophia* (and its subgenus *Mesopholidostrophia*), *Phragmostrophia*, *Radiomena*, *Teichostrophia*, and *Telaeoshaleria*, but not *Lissostrophia*, although they synonymized *Mesolissostrophia* with *Mesopholidostrophia* since their type species were deemed conspecific. In their subsequent revision, Harper and Boucot (1978) considered the Pholidostrophiidae as of familial rank, with the subfamilies Pholidostrophiinae and Teichostrophiinae, and erected the Lissostrophiidae to include *Lissostrophia* alone, although they had removed *Nadiastrophia* to the Douvillinidae and erected a further new family for *Telaeoshaleria*. We have reviewed all these genera in relationship to all other unrelated genera and have come to the conclusion that there is no validity in the previously published concept of the family or subfamily erected around *Pholidostrophia*. The genera can be grouped elsewhere as follows: (1) *Pholidostrophia*, *Lissostrophia* and *Parapholidostrophia* are placed with the Strophodontidae, based on the distinctive shapes of the ventral valve muscle field and also the trans-muscle ridges, central median septum and side septa in the dorsal valve. Thus we consider the family and subfamily name to be a junior synonym of Strophodontidae Caster, 1939; (2) *Eopholidostrophia* and *Mesopholidostrophia* are placed in the Eopholidostrophiidae fam. nov. (see below); (3) *Nadiastrophia*, *Phragmostrophia*, *Radiomena*, *Teichostrophia* (and its synonym *Ancylostrophia*), and *Telaeoshaleria* are placed within the Douvillinidae, also based on the ventral muscle field and dorsal internal structures.

One reason why *Pholidostrophia* and *Mesopholidostrophia* have been considered related in the past has been because of their notable nacreous shells, the only ones in the entire Strophomenoidea; however that shell condition is seen developed polyphyletically elsewhere in the Brachiopoda and in the Mollusca, Bryozoa, and other phyla.

Family EOPHOLIDOSTROPHIIDAE fam. nov.

Diagnosis. Denticles on hinge line or denticular plates. Moderately to strongly concavo-convex. Triangular ventral valve muscle field very weakly impressed, open anteriorly and with no muscle bounding ridges except for a short distance posterolaterally. No radial ridges within the ventral muscle field, unlike the Leptostrophiidae. Cardinal process lobes small, separate and ventrally directed. Short thin socket ridges. Side septa absent.

Type genus. *Eopholidostrophia* Harper *et al.* 1967.

Included genera. *Eopholidostrophia*, *Origostrophia* Mitchell, 1977, and *Mesopholidostrophia* Williams, 1950 (with its junior synonym *Mesolissostrophia* Williams, 1950). Range: Ashgill (Rawtheyan) to Ludlow (Gorstian).

Discussion. Although *Eopholidostrophia* is similar to early leptostrophiids in its muscle field shape and cardinalia, the gross differences in shell-shape and covexity between it and *Eostropheodonta* and its relatives indicate that they were derived from different stocks within the Rafinesquininae, and thus *Eopholidostrophia* and *Eostropheodonta* should be assigned to separate families to prevent the Leptostrophiidae from becoming a polyphyletic taxon. The strong dental plates of *Eostropheodonta* are absent in *Eopholidostrophia*. The Ashgill species *Eopholidostrophia matutinum* and *E. fragilis* have more flaring and narrower denticular plates than contemporary *Eostropheodonta*, such as the widespread *E. hirnantensis* (Text-fig. 18), and thus the denticulation of *Eopholidostrophia* progressed along the standard evolutionary path separately from *Eostropheodonta* and its descendants *Palaeoleptostrophia* and *Brachyprion*.

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APPENDIX

Strophomenoids with crenulated teeth and sockets

In this list the following symbols are used: ∗, we have seen the specimens; crenulations have been reported or observed in ⊙ the ventral valve, ○ the dorsal valve and ● both valves.

In the **Strophomenidae** we have seen crenulations in (1) ● *Strophomena planumbona* (Hall), the type species of *Strophomena* (Spjeldnaes 1957, fig. 3E–G, and ∗AMNH 30248; Plate 1, figs 10–11); (2) ⊙ *S. bilix* (Lamont) [syn. *S. cancellata* (Portlock)] (Mitchell 1977, p. 98); (3) ○ *S. filitexta* (Hall) (∗AMNH 918/5(*a*); Plate 1, fig. 8); (4) ⊙ *S. neglecta* (James) (Spjeldnaes 1957, pl. 12, fig. 8); (5) ● *S. satterfieldi* Amsden (1974, p. 51, pl. 23, fig. 2*a*–*b*); (6) ● *Bellimurina tenuicorrugata* (Reed) (Williams 1962, p. 205); (7) ● *Biparetis paucirugosus* Amsden (1974, pl. 21, fig. 1*c*, *p*–*q*; pl. 22, fig. 1*b*); (8) *Drummuckina donax* (Reed) (∗B7290); (9) ⊙ *Furcitella plicata* Cooper (∗USNM 117751*a*); (10) ○ *Iberomena sardoa* (Vinassa) (Villas 1985, pl. 22, fig. 8; Havlíček *et al.* 1987, pl. 9, fig. 13); (11) ⊙ *Infurca tessellata* Percival (1979, p. 185, pl. 2, figs 14–15); (12) ● *Katastrophomena woodlandensis* (Reed) (∗BC2170; Plate 1, fig. 12); (13) ⊙ *Longvillia grandis* (J. de C. Sowerby) (∗B8528); (14) ⊙ *Luhaia vardi roomusoksi* Sheehan (1987, p. 40); (15) ○ *Maakina kulinnensis* Andreeva (*in* Nikiforova and Andreeva 1961, pl. 33, figs 5, 7) [this species has strong denticles in the anterior face of the sockets]; (16) ● *Macrocoelia stenomuscula* Laurie (1991, p. 72, fig. 41B); (17) ● *Oepikina septata* Salmon, the type species of *Oepikina* (USNM 117829*c*; Plate 2, fig. 8; Plate 3, figs 6–7); (18) ⊙ *Oepikina speciosa* Cooper (1956, pl. 249, fig. 7); (19) ○ *Oepikina? walliensis* Percival (1991, p. 149) [the cardinalia of this species is of the *Strophomena* group]; (20) ⊙ *Pseudostrophomena reclinis* Rõõmusoks (∗BB91296); (21) ⊙ *Rhipidomena tennesseensis* (Willard) (Cooper 1956, pl. 253, figs 12–13); (22) ● *Trigrammaria ampla* Percival (1991, p. 149, fig. 15–4); (23) ⊙ *Trigrammaria virve* Rõõmusoks (1985, p. 134).

In the **Rafinesquinidae** we have observed crenulations in both subfamilies; in the **Rafinesquininae**: (1) ○ *Rafinesquina alternata* (Hall), the type species of *Rafinesquina* (∗B39912); (2) ○ *Hedstroemina fragilis* (Bancroft) (∗BB73550); (3) ○ *Hedstroemina* sp. (Bergström 1968, p. 13); (4) ○ '*Macrocoelia*' *llandeiloensis elongata* Lockley and Williams (∗BB92421) [this species should be assigned to the rafinesquinids, but *Macrocoelia* is a strophomenid]. In the **Leptaeninae**: (1) ○ *Leptaena contermina* Cocks (1968, p. 6, fig. 10); (2) ○ *L. depressa* (J. de C. Sowerby; Havlíček 1967, pl. 16, fig. 16; ∗B43366 and others; (3) ○ *Leptaena minuta* Kiaer (Mitchell 1977, p. 106, pl. 23, fig. 10); (4) ○ *L.* cf. *ordovicica* Cooper (Williams 1962, p. 198); (5) ● *L. reedi* Cocks (Temple 1970, p. 46); (6) ○ *Leptaena rugosa* Dalman, the type species of *Leptaena* (Bergström 1968, p. 15; Mitchell 1977, p. 109, pl. 23, figs 16–17, 25–26); (7) ○ *Leptaenopoma trifidum* Marek and Havlíček (Bergström 1968, p. 16, text-fig. 8); (8) ● *L. valentia* Cocks (Temple 1970, pl. 44); (9) ○ *Leptaena ventricosa* Williams (1963, p. 462; with sockets striated); (10) ○ *Kosomena kosia* Havlíček (*in* Havlíček and Štorch 1990, p. 71); (11) *Leptagonia analoga* (Williams 1965, p. H394); (12) *Mackerrovia lobatus* (Lamont and Gilbert) (∗BC50573).

In the **Glyptomenidae** there are crenulations in: (1) ● *Mjoesina moorei* Mitchell (1977, p. 102, pl. 21, figs 11, 13, 16); (2) ○ *M. rugata*; and (3) ○ *M. rugata plana* Williams (1962, p. 208). In the **Leptaenoideidae**: (1) ● *Liljevallia amorpha* Zhang (1989, p. 107, pl. 5, figs 13, 15–17); (2) ⊙ *Leptaenisca concava* Hall (Yale Peabody Museum 28115); (3) *Leptaenomendax chaconae* Gracia-Alcade (1978, p. 256).

UPPERMOST ORDOVICIAN TO LOWER SILURIAN GRAPTOLITE BIOSTRATIGRAPHY OF THE WYE VALLEY, CENTRAL WALES

by JAN ZALASIEWICZ *and* STEVE TUNNICLIFF

ABSTRACT. The graptolite biostratigraphy of the *persculptus* to *magnus* Biozone interval (upper Hirnantian to lower Aeronian) in the Wye valley near Rhayader, central Wales, is described. Possible refinements to the graptolite zonal scheme are indicated, including informal subdivisions of the *acuminatus* and *acinaces* Biozones. Quantitative faunal assessment indicates that diplograptid:monograptid ratios are useful in indicating stratigraphical level. Selected taxa are described, including three new species, *Normalograptus? wyensis*, *Pseudoglyptograptus barriei* and '*Orthograptus*' *cabanensis*.

THE upper Hirnantian to lower Aeronian sequence of central Wales is rich in graptolites, having been laid down in predominantly anoxic, benthos-free bottom conditions. Turbidites, mostly mud-dominated, are interspersed with graptolite-bearing laminated hemipelagic deposits (Cave 1979). The biostratigraphy of the sequence was studied in the early part of this century, by H. Lapworth (1900), Jones (1909), and Davies (1929) in particular, and a number of the standard graptolite zones were established in this region (see Rickards 1976; Zalasiewicz 1990). Though a few later studies (Sudbury 1958; Packham 1962) examined parts of the sequence in detail, further refinement of the graptolite biostratigraphy of this interval took place mostly outside Wales in the UK (the Southern Uplands – Toghill 1968; Howgill Fells – Rickards 1970; the Lake District – Hutt 1974–5) and abroad (Germany – Stein 1965; Schauer 1971; the CIS – Koren' 1973 and references therein; Bornholm – Bjerreskov 1975; China – Chen 1984; the Canadian Arctic – Melchin 1989). The only recently published biostratigraphical section through this interval in Wales is by Baker (1981).

This study comprises a systematic re-examination of the graptolite biostratigraphy of the *persculptus-magnus* Biozone interval in the Wye valley section near Rhayader, augmented by data from other sections. The work was carried out in the course of recent BGS mapping of the Rhayader and Llanilar district of central Wales, and a detailed account of the stratigraphy is given in Davies *et al.* (in press). Ranges of species are given, together with descriptions and illustrations of new taxa and of established taxa in which new morphological information was discerned. Three new species are described. All figured material is lodged with the British Geological Survey, Keyworth, unless otherwise indicated.

STRATIGRAPHY

The interval studied is represented by the argillaceous Cwmere Formation (Cave and Hains 1986) and equivalent arenaceous formations (see Davies *et al.* in press). These comprise turbidite deposits with interspersed graptolite-bearing laminated hemipelagites.

The Cwmere Formation is underlain by the Yr Allt Formation which comprises mainly slumped deposits laid down during the end-Ordovician glacio-eustatic regression (Davies *et al.* in press). The transition from the Cwmere to the overlying Derwenlas Formation is marked by a change from laminated 'anoxic' to burrowed and oxidized hemipelagites, from which graptolites are generally absent. Higher levels within the Derwenlas Formation, though, include graptolitic levels associated with laminated hemipelagites.

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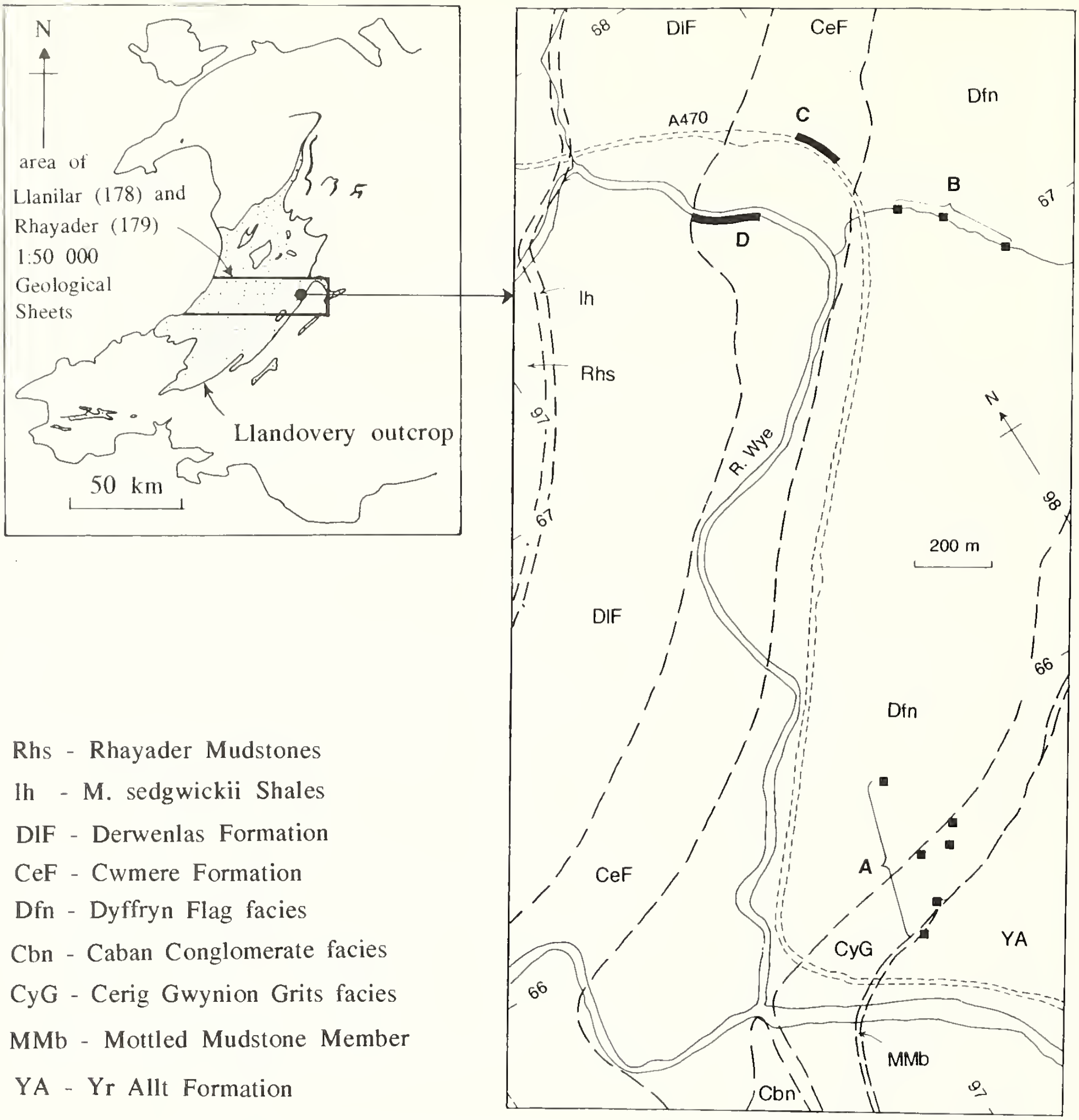


TEXT-FIG. 1. Location of the area examined, and geological map of the Wye valley near Rhayader (after Davies *et al.* in press); taxa from localities A–D are shown in Text-fig. 3.

The lower part of the sequence in the Wye Valley around Rhayader (Text-figs 1, 3) comprises turbidite sandstones (the Cerig Gwynion Grits and Dyffryn Flags facies of the Caban Conglomerate Formation) and these pass up into turbidite mudstones of the Cwmere Formation, which contain increasing proportions of laminated hemipelagite upwards, up to 50 per cent near the top of the sequence.

BIOSTRATIGRAPHY

All the standard graptolite zones of the uppermost Hirnantian, Rhuddanian and Lower Aeronian (Rickards 1976) have been recognized. Text-figure 2 shows the biozonal distribution of species within the Llanilar–Rhayader district (for further details see Davies *et al.* in press) and Text-figure 3 shows the succession in the Wye Valley section.

Normalograptus? persculptus *Biozone*

This has been recognized in the Mottled Mudstone Member of the Yr Allt Formation and within the overlying Cerig Gwynion Grits. It is characterized by the presence of the zone fossil and abundance of the narrow related form *N? parvulus* (= *Glyptograptus* cf. *persculptus* (*sensu* Williams 1983) together with long-ranging climacograptid species of *Normalograptus* such as *N. normalis*.

Parakidograptus acuminatus *Biozone*

In the Wye valley section (Text-fig. 3), the base of the *acuminatus* Biozone occurs *c.* 40 m above the top of the Cerig Gwynion Grits. It is marked by the incoming of *Akidograptus ascensus*, occurring together with *N? parvulus* and other normalograptids. *Parakidograptus acuminatus* replaces *Akidograptus ascensus* at higher levels in the zone; this is consistent with the informal two-fold zonal subdivision recognized by Rickards (1976), with some authors recognizing two zones at this level based on the relative abundances of these two species (e.g. Bouček, 1953; Tomczykowa 1988). *Normalograptus? persculptus* and *N? parvulus* may not extend to the top of the *acuminatus* Biozone. The former co-occurs with *P. acuminatus* in the Wye valley section (Text-fig. 3), where it is present as a 'late' morphotype, with no median septum on the reverse side (Text-fig. 5B; cf. Davies 1929). Neither *N? persculptus* nor *N? parvulus* have been found with other presumed high *acuminatus* Biozone assemblages, which contain *P. acuminatus* (but not *A. ascensus*) and '*Orthograptus*' *cabanensis* in a section (SN 9198 6317 to SN 9195 6283) adjacent to the Caban-coch reservoir.

Atavograptus atavus *Biozone*

This was recognized originally in the Wye section at Rhayader by H. Lapworth (1900) who termed it the *Monograptus tenuis* Biozone due to a misidentification of the zone fossil. Jones (1909), working in the Rheidol Gorge, rectified this by the proposal of the name *Monograptus* (= *Atavograptus*) *atavus* for this graptolite. Re-examination of Lapworth's type section (Text-fig. 3) suggests that only the upper part of the *atavus* Biozone (little more than 5 m thick) is currently exposed. The assemblage is characterized by *Atavograptus atavus*, *A. gracilis*, and species of *Normalograptus*.

Lagarograptus acinaces *Biozone*

This biozone is 65 m thick within the Wye valley (Text-fig. 3). Two successive assemblages were noted. The lower assemblage contains *L. acinaces* accompanied by normalograptids of a lower Rhuddanian aspect (*N. normalis*, *N. rectangularis*). This is present in the lower 15 m of the *acinaces* Biozone in the Wye valley. The upper assemblage contains *L. acinaces*, accompanied by a more diverse fauna including *Pribylograptus incommodus*, *Pr. sandersoni*, *Pristiograptus fragilis pristinus*, *Coronograptus cyphus cyphus*, *Dimorphograptus confertus confertus*, *Pseudoclimacograptus hughesi* (*sensu* Bulman and Rickards 1968), *Rhaphidograptus toernquisti*, and *Glyptograptus tamariscus*.

Coronograptus cyphus *Biozone*

This was defined originally by H. Lapworth (1900) in the Wye valley section (Text-fig. 3). Subsequent work, however, has shown that the zone fossil, *Coronograptus cyphus cyphus*, ranges down into the *acinaces* Biozone, so that different criteria are needed to determine the *acinaces-cyphus* zonal boundary. Here, the base of the *cyphus* Biozone is drawn at the incoming of monograptids of the *revolutus/austerus* groups (one of the criteria used by Rickards 1976), giving a thickness of the *cyphus* Biozone in the Wye valley of 45 m. Adoption of a '*revolutus* Biozone' in place of the *cyphus* Biozone is a possibility, and this nomenclature has been adopted on Bornholm (Bjerreskov 1975); the appearance of abundant *revolutus/austerus* forms is also clear on the only other recently published graptolite range-chart through Rhuddanian strata in Wales (the Llanystumdwy section: Baker 1981). Other graptolites characteristic of this interval include *Coronograptus gregarius* subspecies (e.g. Text-fig. 8A–B), *Atavograptus strachani* (Text-fig. 10D) and *Normalograptus? wyensis*.

STAGES	Hirnantian	Rhuddanian				Aeronian	
BIOZONES	persculptus	acuminatus	atavus	acinaces	cyphus	triangulatus	magnus
Normalograptus? persculptus	X	L					
Normalograptus? parvulus	A	L					
Normalograptus normalis	A	A	X	X			
Normalograptus angustus	X	X	X	X			
Glyptograptus avitus	X						
Normalograptus medius	X	X	X	cf.	?		
Diplograptus aff. modestus primus	X						
Akidograptus ascensus		L					
Parakidograptus acuminatus		U					
'Orthograptus' cabanensis sp. nov.		U					
Rhaphidograptus extenuatus			L				
Atavogratus atavus			X	X	X		
Atavograptus gracilis			X				
Normalograptus rectangularis			X	X	X	X	
Lagarograptus acinaces				A	X		
Glyptograptus aff. *incertus* sensu Hutt 1974				*	*		
Dimorphograptus confertus confertus				U			
Metaclimacograptus hughesi sensu Bulman & Rickards				U			cf
Cystograptus vesiculosus				U			
Pribylograptus sandersoni				U			
Pristiograptus fragilis pristinus				U			
Glyptograptus tamariscus tamariscus				U			cf. →
cf. *'Orthograptus' mutabilis*				U	X		
Rhaphidograptus toernquisti				U(A)	A	A	X
Coronograptus cyphus cyphus				U	X		
Pribylograptus incommodus				U			
Atavograptus cf. *strachani*					X	?	
Monograptus ex gr. *revolutus/austerus*					X	X	
Monograptus austerus cf. *austerus*					X		
Monograptus cf. *sudburiae*					X		
?Monoclimacis sp.					R		
Coronograptus gregarius aff. *minisculus*					X		
Normalograptus? wyensis sp. nov.					X		
Glyptograptus tamariscus cf. *varians*					X		
Pribylograptus cf. *argutus argutus*					X	X	?
Metaclimacograptus undulatus					X	X	X →
Coronograptus gregarius gregarius					?U	X	X →
Monograptus triangulatus triangulatus						X	
Monograptus triangulatus extremus						R	
Monograptus ?aff. *walkerae*						X	
Monograptus sp. 1						X	
Pristiograptus concinnus						X	
Monograptus ex gr. *revolutus*						X	
Monograptus communis communis						X	
Glyptograptus? alternis						X	
aff. *Pseudoglyptograptus vas*						X	
Rastrites sp.						U	
Monograptus communis rostratus						U	
Glyptograptus cf. *enodis enodis*						?	X
Monograptus triangulatus fimbriatus						U	A
Normalograptus? magnus							A
Rastrites longispinus							X →
aff. *Atavogratus strachani*							R
Monograptus chrysalis							X
Pseudoglyptograptus barriei sp. nov.							A

TEXT-FIG. 2. For legend see facing page.

Monograptus triangulatus *Biozone*

Strata referable to the *M. triangulatus* Biozone are 20 m thick in the Wye valley (Text-fig. 3). Triangulate monograptids and *Coronograptus gregarius gregarius* characterize this biozone. A low-diversity interval, in which no triangulate monograptids have been found, is succeeded by faunas including *M. triangulatus extremus*, indicative of a middle *triangulatus* Biozone level (cf. Sudbury 1958; Rickards 1976). *Pristiograptus concinnus*, *Monograptus communis* subspecies, and *Monograptus triangulatus fimbriatus* (= *M. pectinatus* Richter according to Bjerrskov 1975) appear in the upper part of the biozone.

Normalograptus? magnus *Biozone*

The upper part of the Cwmere Formation in the Rhayader/Llanilar district lies within the *magnus* Biozone, 14 m having been proved in the Wye valley (Text-fig. 3). Graptolites from the uppermost Cwmere Formation have also been recovered from the Tynygraig railway cutting (SN 6859 7012) and from a roadside section (SN 7324 7203) near Ysbyty Ystwyth, Dyfed.

The presence of the zone fossil is the principal criterion, and this graptolite is characteristically associated with *Monograptus triangulatus fimbriatus*, *Pseudoglyptograptus barriei* and *Monograptus chrysalis*.

QUANTITATIVE DISTRIBUTION OF MAJOR GRAPTOLITE GROUPS

Graptolite faunas composed exclusively of long-ranging diplograptids of *normalis* type (*Normalograptus*) are common in the Cwmere Formation. Thus, using species ranges alone, imprecise dates spanning much of the Rhuddanian/early Aeronian are obtained. However, this stratigraphical interval is characterized by a marked and progressive increase in graptolite diversity, bringing in the monograptids together with other diplograptid groups. Normalograptid-dominated assemblages should therefore be more common at lower stratigraphical levels, and so could provide a guide to age.

Here, the gross compositions of systematic collections made in the Wye valley (see Text-fig. 3) are compared, to indicate the likelihood of *Normalograptus*-dominated assemblages occurring within different graptolite biozones.

Graptolites from the *persculptus* to the top of the *triangulatus* Biozone were considered. Collections were made at forty two levels in the section, the number of specimens in each collection ranging from two to more than eighty (Text-fig. 4). These were assigned to one of five categories, selected to show the gross composition of the fauna in the most practicable way.

1. *Normalograptus/Glyptograptus*. This category, characterized by proximal end development, includes graptolites of the *normalis* group, together with related forms including those related to *Glyptograptus tamariscus*.

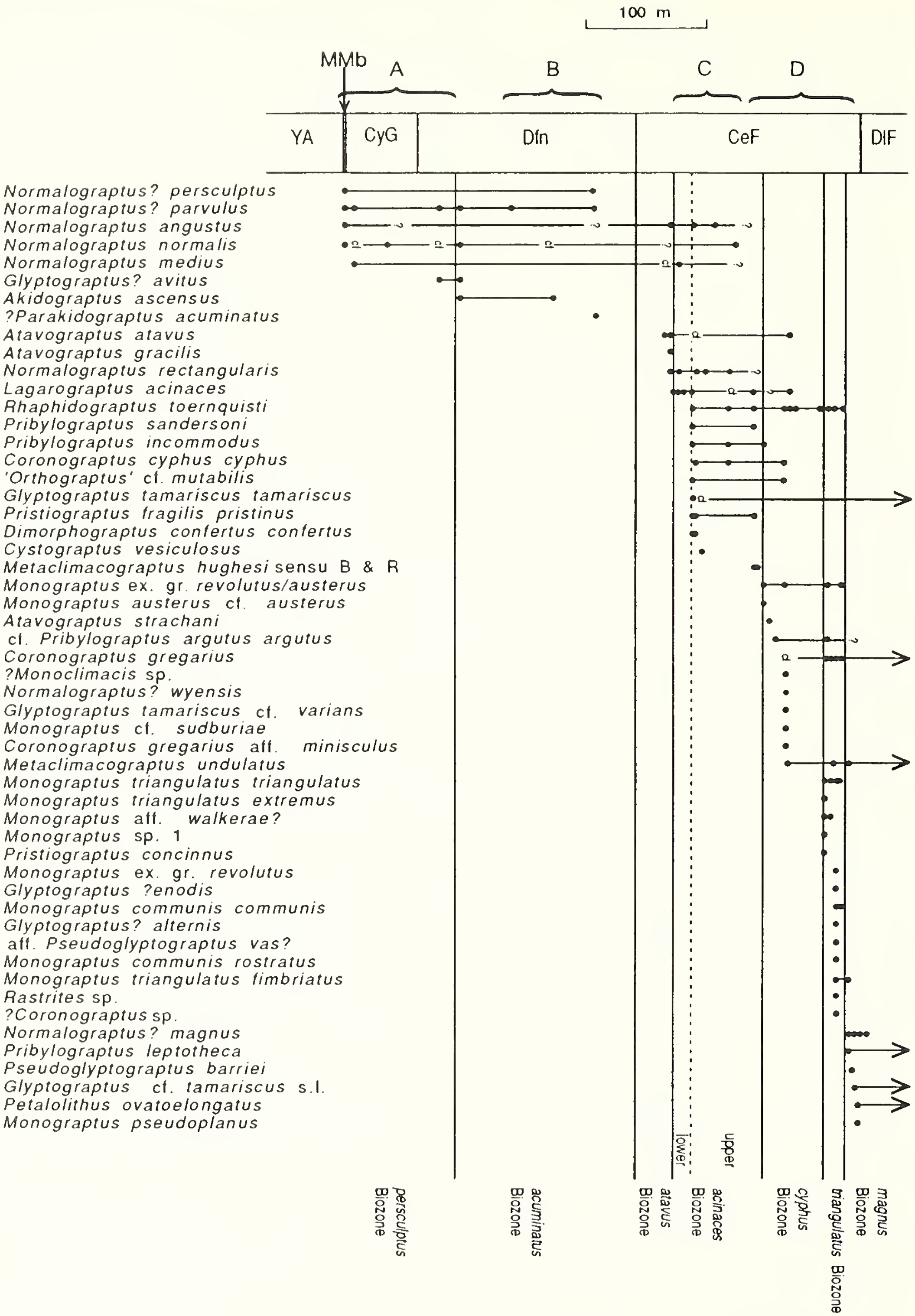
2. Other diplograptids including *Akidograptus*, *Parakidograptus*, *Pseudoclimacograptus*, and *Dimorphograptus* (but excluding *Rhaphidograptus* – see below).

3. *Rhaphidograptus*. A separate category was erected for this genus because of the observed abundance of *R. toernquisti* from the *acinaces* Biozone upwards.

4. *Rhaphidograptus/Normalograptus* undivided. This category is needed because of the difficulty of distinguishing distal fragments of *R. toernquisti* from those of normalograptids, particularly *N. rectangularis*.

5. Monograptids.

TEXT-FIG. 2. Range of graptolite taxa in the Cwmere Formation of the Llanilar–Rhayader district (after Davies *et al.* in press). X, taxon present; A, taxon abundant; R, taxon rare; U, taxon from upper part of zone; L, taxon from lower part of zone; *, taxon from undetermined level within interval marked. Arrow indicates that taxon ranges beyond the limits of this range chart. Abundance estimates are subjective.



TEXT-FIG. 3. For legend see facing page.

The number of graptolites falling into each category was counted for each collected level, converted into a percentage, and then plotted on to a composition-diagram (Text-fig. 4). The total number of graptolites collected at each level was also recorded, and plotted alongside.

The data clearly demonstrate the upward change in overall composition of the graptolite faunas. The *persculptus* and *acuminatus* Biozones are dominated by graptolites of the *normalis* group, and many collections contain nothing else. In the *acuminatus* Biozone, the zone-determining *Akidograptus* and *Parakidograptus* tend to be of sporadic occurrence, and to form only a small part of assemblages.

A marked change occurs at the base of the *acinaces* Biozone. Above this level, other graptolite categories (notably monograptids and *Rhaphidograptus*) form an important part of the assemblages. Out of twenty one collections which included ten or more graptolite specimens, only one did not include any monograptids, and there were none in which neither monograptids nor *Rhaphidograptus* were observed. Out of twenty seven collections containing five or more graptolites, there were only two in which neither monograptids nor *Rhaphidograptus* were observed, and these were both of pre-*cyphus* Biozone age.

Thus, it appears that the gross composition of assemblages can be used, cautiously, to give some evidence of age. Such quantitative comparison of assemblages is not a standard means of correlation in Lower Palaeozoic strata (though it is more commonly used in younger strata, particularly in the Quaternary). The patterns of gross faunal change described here may be expected to provide moderately reliable indications of age within the Welsh Basin, but probably would not help correlation between regions or across facies boundaries.

SYSTEMATIC PALAEONTOLOGY

Repositories. The prefixes BU and SM denote respectively collections of Birmingham University, and the Sedgwick Museum, Cambridge; specimens with prefixes DJ, GSM, JZ, JZB, and Pg are housed at the British Geological Survey, Keyworth, Nottingham, as are other specimens or collections not specified by number.

Genus GLYPTOGRAPTUS Lapworth, 1873, *emend.* Melchin and Mitchell, 1991

Type species. Original designation; *Diplograptus tamariscus* Nicholson, 1868.

Glyptograptus? alternis (Packham, 1962)

Text-figure 6E

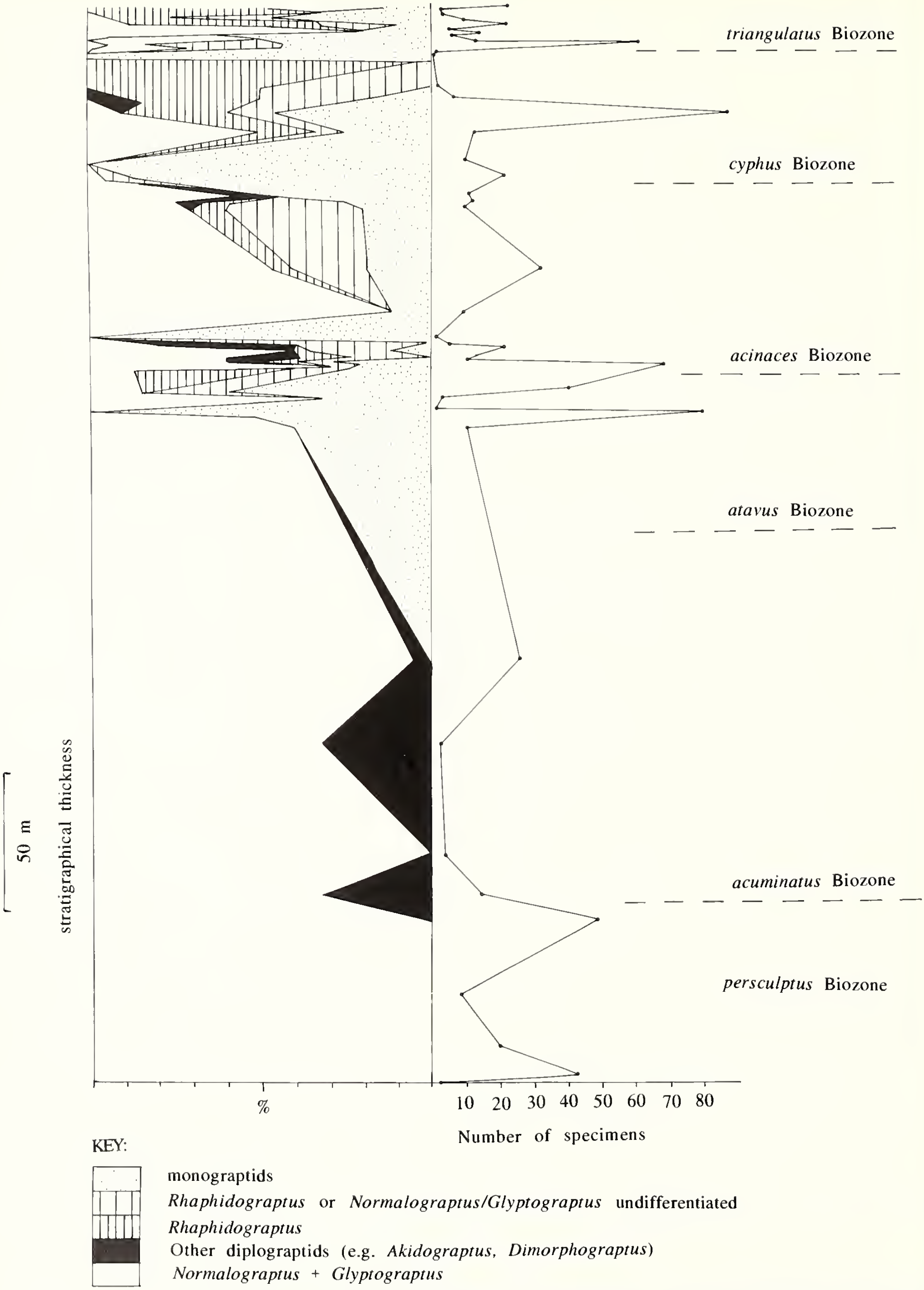
1962 *Climacograptus alternis* sp. nov.; Packham, p. 521, pl. 72, fig. 5, text-fig. 4*f*.
1972 *Pseudoglyptograptus* sp. 3; Rickards, p. 279, text-fig. 3.1.

Holotype. SM A24957, figured by Packham (1962, pl. 72, fig. 5), from the *triangulatus* Biozone of the Rheidol Gorge, Wales.

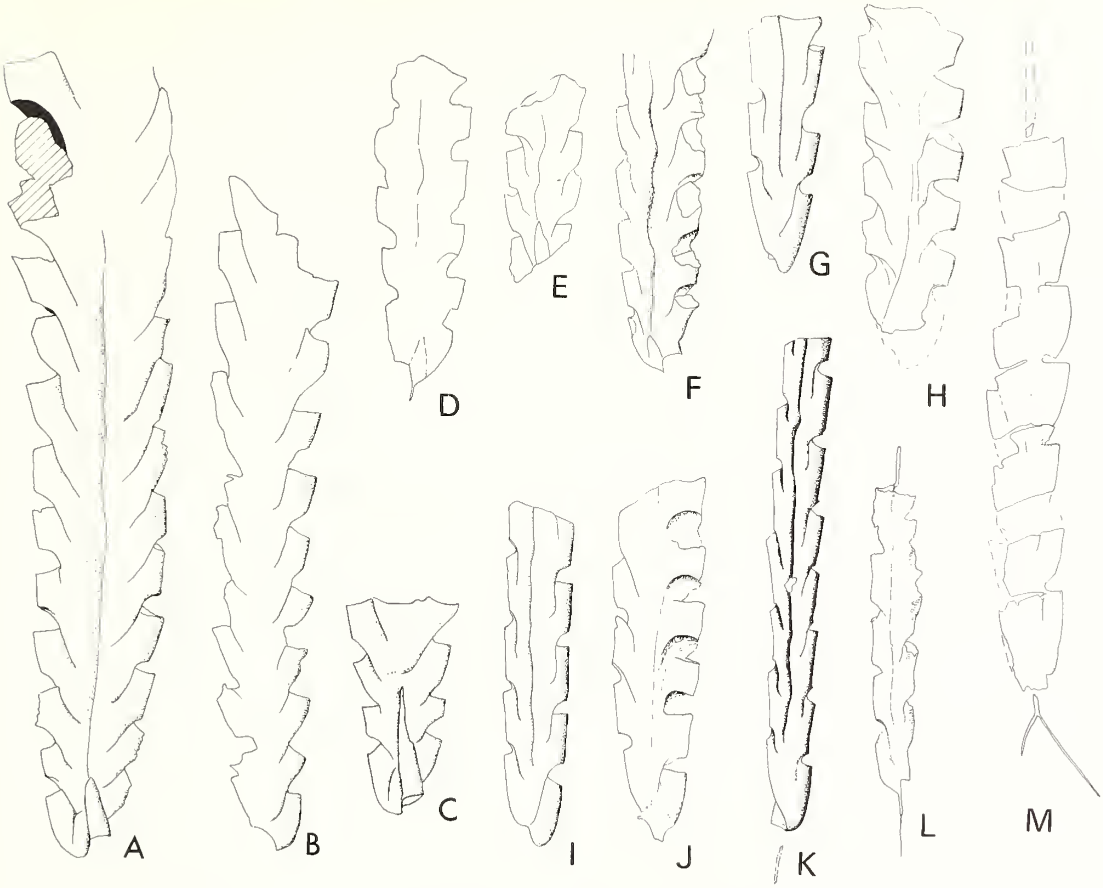
Material. One complete specimen, two incomplete fragments, all preserved in relief, from the *triangulatus* Biozone of the Wye valley section (Text-fig. 3).

Description. Aseptate diplograptid, increasing in width from 0·6 mm proximally to 1·0 mm at theca five and 1·3 mm at theca ten. 2TRDs (= two theca repeat distances; Howe 1983) range from 1·6 mm proximally to 1·8 mm distally. The obverse side has been recognized for the first time. The sicula is visible for 1·1 mm, and

TEXT-FIG. 3. Range-chart of graptolite taxa through the Wye valley section, Rhayader. YA, Yr Allt Formation; MMb, Mottled Mudstone Member; CyG, Cerig Gwynion Grits facies; Dfn, Dyffryn Flags facies; CeF, Cwmere Formation; DlF, Derwenlas Formation. ●, identified; cf., qualified identification; ?, doubtful identification.



TEXT-FIG. 4. Quantitative distribution of major graptolite groups through the Cwmere Formation in the Wye valley section.



TEXT-FIG. 5. A–C, *Normalograptus? persculptus* (Elles and Wood) *s.s.*; all specimens on block JZ 417; *acuminatus* Biozone; Wye valley section (SN 9806 6709). D–J, *Normalograptus? parvulus* (H. Lapworth). D, BU 1293, lectotype; *persculptus* or *acuminatus* Biozone; Gwastaden, Rhayader district. E, BU 829, H. Lapworth coll. F, JZ 2354; lower *acuminatus* Biozone; Nant Paradwys (SN 8919 6702). G, I, lower *persculptus* Biozone; Cerig Gwwynion Quarry (SN 8919 6702). G, JZ 4857; I, JZ 4861. H, JZ 6646; *acuminatus* Biozone; Dolaucothi Gold Mine (SN 6620 4015). J, JZ 8687; *persculptus* Biozone; roadside quarry (SN 8855 6268), near Claerwen Reservoir. K–L, *Normalograptus miserabilis* (Elles and Wood). K, DJ 8828; *acuminatus* Biozone; Wye valley section (SN 9805 6719). L, JZ 2460; *acuminatus* Biozone; east shore of Caban-coch Reservoir (SN 9223 6391). M, *Glyptograptus? avitus*. JZ 4813; Davies, upper *persculptus* Biozone; trackside exposure, Cerig Gwynion Quarry (SN 9722 6577). All figures are × 10.

extends to just above the theca 1^1 aperture; its lateral wall is free for just over half its length below theca 1^2. The thecae approach a glyptograptid morphology, with straight interthecal septa and rounded genicula. The apertures are not well preserved, but appear somewhat everted.

Discussion. The material appears conspecific with the single specimen described by Packham (1962), though there are slight dimensional differences; the latter is a little broader proximally and slightly more densely thecate. The length of the lateral sicula wall exposed beneath $\mathrm{th}1^2$ suggests a relatively high origin for that theca, and thus affinity with the genus *Glyptograptus* rather than *Normalograptus* (see discussion of the latter below).

The material also seems conspecific with the specimen figured by Rickards (1972) as *Pseudoglyptograptus* sp. 3. In that specimen, some distal thecae show concave supragenicular walls;

this feature is not obvious in the material described here. If it is not due to preservation, it may indicate that Rickards' generic determination is more appropriate for this species.

All material assigned to this taxon comes from the middle or upper part of the *triangulatus* Biozone (Packham 1962; Text-fig. 3), making this rare but conspicuous aseptate species of potential biostratigraphical importance.

Glyptograptus? avitus Davies, 1929

Text-figure 5M

Discussion. The scarce material agrees well with Williams' (1983) detailed redescription, the best preserved specimen (Text-fig. 5M) showing the commonly developed bifurcating virgella. As Williams noted, the link with *Parakidograptus* suggested by Davies (1929) seems unlikely. Thecal morphology seems similar to that of the later *tamariscus* group of glyptograptids (cf. Text-fig. 6F; Packham 1962).

Genus NORMALOGRAPTUS Legrand, 1987, *emend.* Melchin and Mitchell, 1991

Type species. By original designation, *Climacograptus scalaris normalis* Lapworth, 1877.

Discussion. The recognition of a distinctive, pointed, non-spinose proximal end in many Ordovician and most Silurian diplograptids was made by Legrand (1987) and Mitchell (1987). Mitchell included proximal developments of his patterns H and I within an emended genus *Glyptograptus* (type species *G. tamariscus*), while Legrand simultaneously proposed the genus *Normalograptus*, based upon *Climacograptus normalis*. Both these genera included species with climacograptid and glyptograptid thecae, effectively rendering these styles of thecal construction (which form a continuum, see Packham 1962) subordinate to proximal end development in generic assignation. Subsequently, Melchin and Mitchell (1991) separated *Normalograptus* from *Glyptograptus* by recognizing subtly different styles of proximal development in the type species of the two genera. The difference depends primarily upon the level of origin of th1^2, that of *Glyptograptus* originating higher on th1^1 than that of *Normalograptus*; this is equivalent to the difference between Pattern I and Pattern H of Mitchell (1987). Melchin and Mitchell's distinction is recognized here. However, it must be stressed that the distinction is difficult to recognize in non-isolated material, and hence assignation to one or other genus is often tentative.

Normalograptus? persculptus (Elles and Wood, 1907)

Text-figure 5A–C

Discussion. This species has been traditionally assigned to *Glyptograptus* and attributed to Salter. The proximal end morphology, though, closely resembles that of *N. normalis* and hence suggests referral to *Normalograptus*; and, as Salter neither figured nor described this species (see discussion in Williams 1983, p. 624) it is felt here that Elles and Wood (1907) should be regarded as the authors.

The name *N? persculptus* is here restricted to the relatively robust forms (widths of up to 2·0 mm in relief material) that compare closely to the type material. This form is relatively rare in the district. The specimen illustrated in Text-figure 5B, from the lower *acuminatus* Biozone, is aseptate on the reverse side of the rhabdosome. This is consistent with Davies' (1929) observations of a progressive delay in the insertion of the median septum in this species. One specimen (Text-fig. 7C) seems to represent an aberrant specimen; there is no median septum on the obverse rather than reverse side and more of the sicula is exposed than normal. It consists of only three thecal pairs, and its early mortality is perhaps related to this developmental 'mistake'.

Normalograptus? parvulus (H. Lapworth, 1900)

Text-figure 5D–J

1900 *Climacograptus parvulus* H. Lapworth, p. 132, fig. 20*a–c*.
1907 *Mesograptus modestus parvulus* (H. Lapworth) Elles and Wood, p. 264, pl. 31, fig. 12*a*, *non c–d*; text-fig. 181*a*, *non b–c*.
1974 *Glyptograptus persculptus* (Salter); Hutt, p. 28, pl. 6, figs 9–12.
1983 *Glyptograptus* cf. *persculptus* (Salter); Williams, p. 625, pl. 66, figs 4–7.
1983 *Diplograptus* aff. *parvulus* (H. Lapworth) Štorch, p. 164, pl. 4, fig. 4, text-fig. 20.
?1986 *Glyptograptus persculptus* (small form) (Salter); Berry, pp. 140, 141, figs 5*h–j*.
1988 *Scalarigraptus angustus* (Perner); Riva, p. 232, fig. 3*d–h*, ?*j–v*, *non a–c*.

Lectotype. BU 1293 (refigured herein, Text-fig. 5D), from the *persculptus* or *acuminatus* Biozone of the Rhayader district, Wales.

Discussion. *Normalograptus? parvulus* resembles *N? persculptus*, but is commonly shorter, narrower (widths of 0·8–0·9 mm proximally, 1·0–1·5 mm distally) and more densely thecate (2TRDs of 1·4–1·8 mm). It also has moderately well-developed genicular hoods (Text-fig. 5G–J) and some specimens show an undulose medium septum (Text-fig. 5E–F), the latter perhaps a result of differential compaction. It appears conspecific with those forms referred by some authors to 'small forms' of *Glyptograptus persculptus* (e.g. Williams 1983), though some of the latter attain greater lengths. The close thecal spacing of *parvulus* distinguishes it from contemporaneous 'climacograptids' such as *Normalograptus normalis* (Text-fig. 6O) where compression has accentuated the genicula of the former (e.g. Text-fig. 5J). *N. miserabilis* (Text-fig. 5K–L; this species name is retained, pending the provision of a detailed redescription of the possibly conspecific species *angustus*: cf. Riva 1988) is narrower (especially proximally), with a more 'elongated' proximal end, generally more widely spaced thecae, more nearly parallel supragenicular walls, and supragenicular walls that take up a greater portion of the ventral margin (supragenicular wall length to apertural height ratios of *c*. 3:1, compared with 2–2·5:1 for *N? parvulus*). More detailed study may show that *N? parvulus* is one end member of a single, variable species that also includes *N? persculptus*, as some 'normalograptid' populations elsewhere show considerable variation in size. If so, then the name *parvulus* (H. Lapworth, 1900) has priority over *persculptus* (Elles and Wood, 1906). For the present, the two are regarded as distinct taxa.

Normalograptus? magnus (H. Lapworth, 1900)

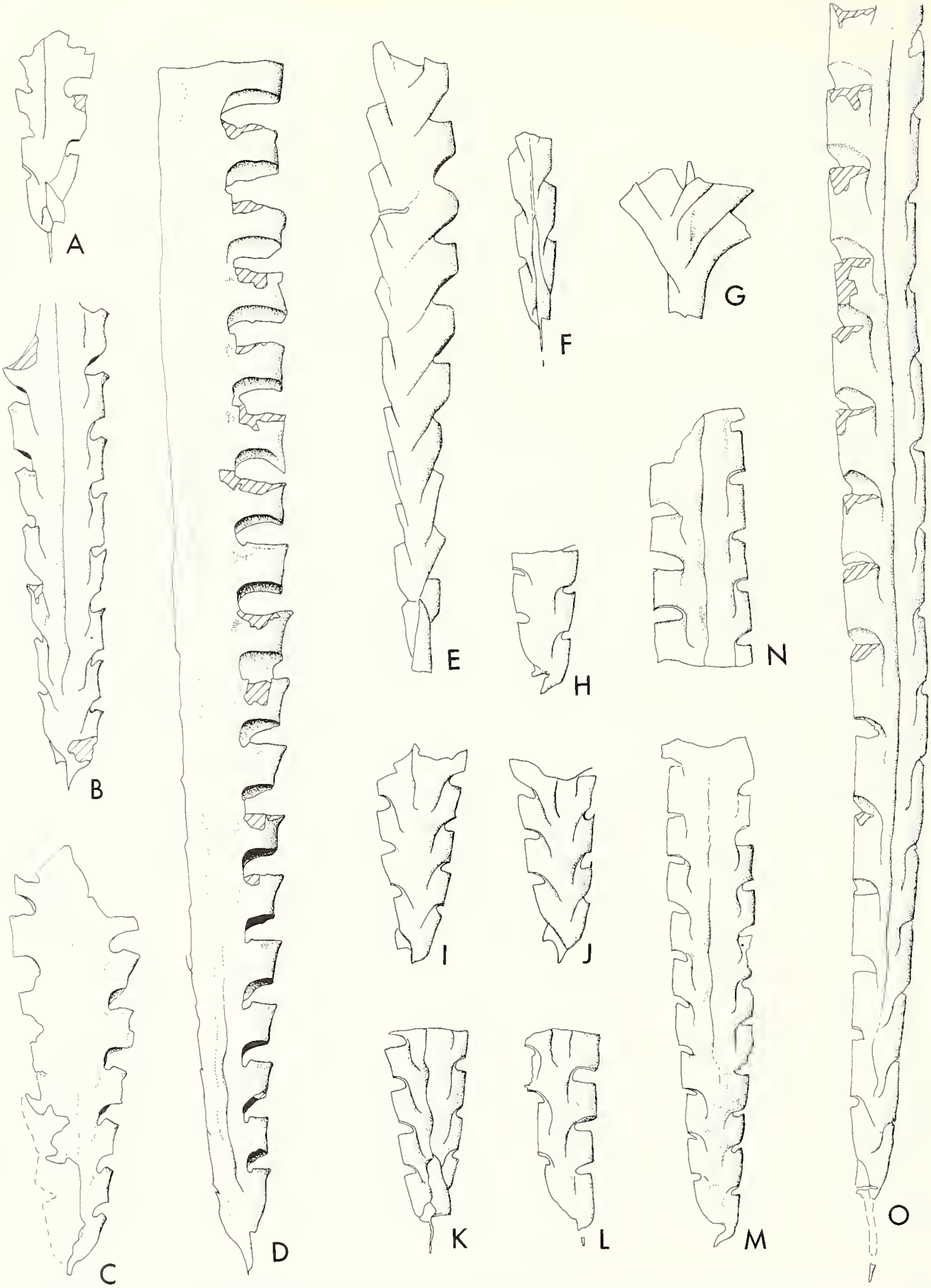
Text-figure 7A–G

1900 *Diplograptus magnus* H. Lapworth, p. 132, text-fig. 21*a–d*.
1907 *Diplograptus* (*Mesograptus*) *magnus* (H. Lapworth) Elles and Wood, p. 266, pl. 31, fig. 14*a–c*, text-fig. 183*a–b*.
1970 *Diplograptus magnus* H. Lapworth; Rickards, p. 35, pl. 3, fig. 8.
1974 *Diplograptus magnus* H. Lapworth; Hutt, p. 32, pl. 5, fig. 6; pl. 6, figs 7–8, 14.
1977 *Diplograptus magnus* H. Lapworth; Rickards *et al*., pl. 3, figs 1, 5 [not described].

Lectotype. BU 1295. Effectively designated Elles and Wood (1907) in their description of pl. 31, fig. 14*a*. The specimen was originally figured by H. Lapworth (1900, text-fig. 21*b*). It originated from the *fimbriatus* (= *magnus*) Biozone of the River Wye section, Rhayader, Wales.

Material. Twenty seven specimens in partial to full relief from the type locality in the Wye valley (Text-fig. 1). Twenty two specimens in slight relief from the *magnus* Biozone in the Tynygraig railway cutting (Text-fig. 1). None of the material shows significant tectonic deformation.

Revised diagnosis. Large diplograptid (s.l.) with proximal end of *Normalograptus* appearance, expanding rapidly from, normally, < 1·0 mm to *c*. 3·0 mm; exceptionally, specimens reach > 4·0 mm in width. Thecae relatively closely spaced (2TRDs of *c*. 1·3–1·4 mm proximally to



TEXT-FIG. 6. A–D, *Pseudoglyptograptus barriei* sp. nov. *magnus* Biozone; Tyn-y-graig railway cutting. A, JZ 8048. B, JZ 8457, holotype. C, JZ 8283. D, JZ 8456. E, *Glyptograptus? alternis* Packham. JZ 9915; *triangulatus* Biozone; Wye valley section. F, *Glyptograptus tamariscus* cf. *varians* Packham. JZB 851; *cyphus* Biozone; Wye

TABLE 1. Dimensions of populations of *Normalograptus? magnus* (in mm).

	Wye Valley	Lectotype	Tynygraig
Width prox.	0·6–0·8	0·7	0·8–1·0
Width th5	1·4–1·8	1·9	1·6–2·0
Width th10	2·0–2·5	2·8	1·7–2·8
Width th20	2·1–3·1	4·1	2·3–3·2
Width max.	?4·1	4·3	3·2
2TRD prox.	1·3–1·5	1·3	1·3–1·5
2TRD th5–7	1·2–1·6	1·5	1·4–1·7
2TRD th10–12	1·4–1·8	1·5	1·5–1·9
2TRD th20–22	1·5–2·0	1·8	1·6–2·1

1·6–2·0 mm distally), approximately glyptograptid throughout, with only slight to imperceptible flattening of genicula distally. Rhabdosome partially septate on the reverse side.

Description. The rhabdosome shows rapid expansion from a moderately slender proximal end; dimensions are given in Table 1. Considerable variation in width was found. The lectotype is the most robust specimen seen, with a maximum width of 4·3 mm; more commonly, maximum widths range from 2·2–3·3 mm. Thecae are sigmoidally curved (approximately 'glyptograptid'), with distinct genicula throughout. There is only slight flattening of the genicula distally; this is more obvious in flattened (Text-fig. 7A–C) than in relief (Text-fig. 7D–G) material. In relief material, apertures appear simple, distally-facing and slightly everted; some flattened material, though, shows traces of what appear to be slender genicular hoods as spine-like processes extending from the geniculum (Text-fig. 7C). The proximal end is of *Normalograptus* aspect, with $th1^1$ growing downwards below the aperture of the sicula before turning upwards, and $th1^2$ growing upwards from close to its origin, leaving part of the sicula wall exposed. The sicula is exposed in the obverse side for 1·4–1·5 mm (Text-fig. 7A, F–G); material where it is 'pressed through' shows it to have a total length of *c*. 2·0 mm (Text-fig. 7E). The median septum is complete on the obverse side, wavy over the first five thecal pairs and subsequently straight (Text-fig. 7F–G); on the reverse side it is partial, starting from the level of the eighth thecal pair in the topotype material (Text-fig. 7D).

Discussion. As noted by Hutt (1974), the lectotype is an abnormally large specimen (> 4 mm wide distally), which underlines the considerable variation in maximum width exhibited.

This species is scarcely biform, and thus is not a true '*Diplograptus*' in the old, form-generic, meaning of this taxon. In this respect, it differs from approximately contemporary robust diplograptids such as '*Diplograptus*' *thuringiaceus* Eisel *in* Münch, 1952, and '*Diplograptus*' *tscherskyi tscherskyi* Obut and Sobolevskaya and thus seems not closely related to them, contrary to the suggestion of Melchin and Mitchell (1991). A more similar species is '*Diplograptus*' *fezzanensis* Desio, 1940 (see also Štorch 1983) which, however, appears to have somewhat more strongly geniculate thecae proximally and a smaller (*c*. 1 mm) sicula.

'*Diplograptus*' *magnus* is the type species of *Neodiplograptus* Legrand, 1987, erected to encompass biform diplograptids with 'keroblastic' (i.e. normalograptid s.l.) proximal structure. However, this redescription shows that *magnus* has only a slightly biform character, scarcely more than in species such as *Normalograptus? persculptus* (compare Text-figures 5A–C and 7D–G) and is morphologically dissimilar to truly biform diplograptids such as '*Diplograptus*' sp. 1 (this paper), '*Glyptograptus*' *sinuatus sinuatus* (Nicholson, 1869) and '*D.*' *thuringiaceus*. Thus, it is unsatisfactory taxon upon which to erect the genus intended, and *Neodiplograptus* is here regarded as a junior synonym of

valley section. G, cf. '*Orthograptus*' *mutabilis* Elles and Wood. JZB 819; *cyphus* Biozone; Wye valley section. H–N, *Normalograptus? wyensis* sp. nov. *cyphus* Biozone; Wye valley section. H, L, JZB 791. I, JZB 817. J, JZB 809. K, JZ 9770. M, JZB 792; latex cast of proximal part of holotype. N, JZ 792 (distal part of M). O, *Normalograptus normalis* (Lapworth). JZ 2306; *acuminatus* Biozone; Nant Paradwys, near Rhayader (SN 8919 6702). All × 10.

Normalograptus. It is not assigned to *Glyptograptus*, as the proximal end of *magnus* appears to resemble more that of the *normalis* group of graptolites than that of the *tamariscus* group (compare Text-figure 6F of *G. tamariscus* cf. *varians*).

Normalograptus? wyensis sp. nov.

Text-figure 6H–N

Derivation of name. After the River Wye, on which the type locality is sited.

Holotype. JZB 792 (Text-fig. 6M–N); from the *cyphus* Biozone of the Wye valley section near Rhayader, Wales (Text-fig. 2).

Additional material. Six other well-preserved rhabdosomes from the type locality.

Diagnosis. A medium-sized, moderately densely thecate and rapidly expanding diplograptid with well-developed genicular hoods and a partial, proximally wavy, median septum.

Description. The longest rhabdosome seen is incomplete distally, and is 12 mm long. Widths are 0·6–0·8 mm proximally, 0·9–1·2 mm at th5 and 1·4 mm at th10, being parallel-sided thereafter. 2TRDs are 1·1–1·5 mm proximally, and 1·6 mm at th10–12. The proximal end appears to be of *Normalograptus* type. The sicula is visible for 0·9 mm of its length on the obverse side, with 0·2–0·4 mm of its lateral wall being free below $th1^2$. The proximal few thecae have sigmoidal interthecal septa, sharp genicula, and supragenicular walls which are slightly inclined in most preservational aspects. The apertures are simple, without lappets, though the ventral apertural wall extends to form a genicular hood (Text-fig. 6L). Distal thecae are similar except that supragenicular walls are parallel to the rhabdosome. The median septum extends from the sicula apex on the obverse side and is wavy over the first four thecal pairs, distally becoming straight; on the reverse side it extends from the base of the fourth thecal pair.

Discussion. This species is placed questionably in *Normalograptus*. The waviness of the median septum proximally, and the eversion of the apertures (through the production of genicular hoods), indicates possible affinities with *Clinoclimacograptus* Bulman and Rickards, 1968. However, the straightness of the supragenicular walls, and their outwards leaning in the proximal part of the rhabdosome, suggest otherwise, while genicular hoods have also been observed in normalograptids such as *N? parvulus* (see above).

Comparison with other species is hampered by the lack of detail concerning thecal and median structures in most published accounts. '*Climacograptus*' *rectangularis*, '*C.*' *stenotelus* Churkin and Carter, 1970, and '*C.*' *medius brevicaudatus* Churkin and Carter, 1970, are similar in their rate of expansion, but reach greater widths. '*Climacograptus*' *janischewskyi* Obut, 1949, expands less rapidly. '*Climacograptus*' *scalaris ferganensis* Obut, 1949, has approximately similar dimensions but (as figured by Melchin 1989) has a straight median septum proximally. *Normalograptus normalis* (Lapworth, 1876) (see Text-fig. 6O) and *N? nirueyensis* (Obut and Sobolevskaya, 1967) have more widely spaced thecae.

Genus PSEUDOGLYPTOGRAPTUS Bulman & Rickards, 1968

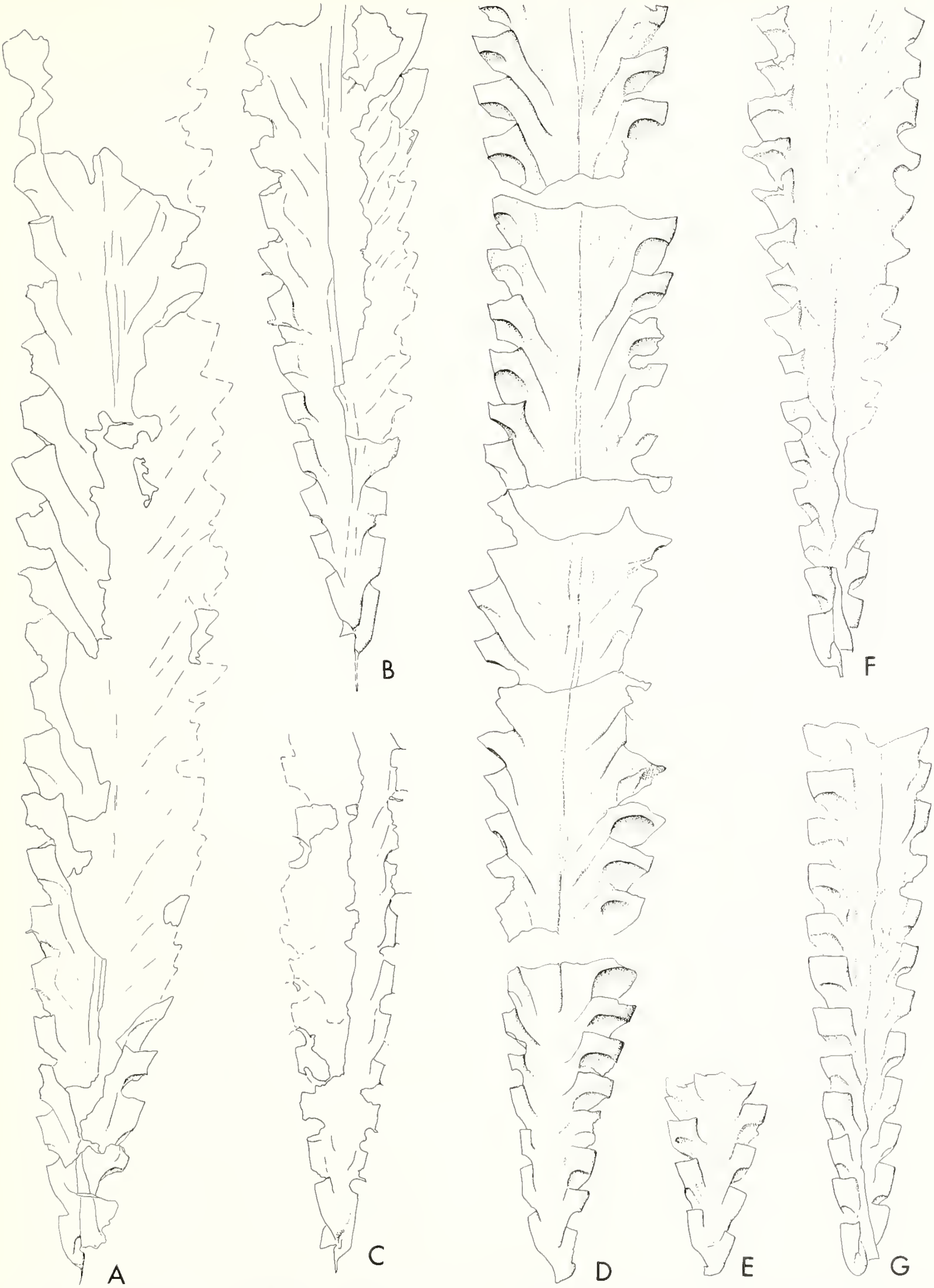
Type species. By original designation, *Glyptograptus* (*Pseudoglyptograptus*) *vas* Bulman and Rickards, 1968.

Pseudoglyptograptus barriei sp. nov.

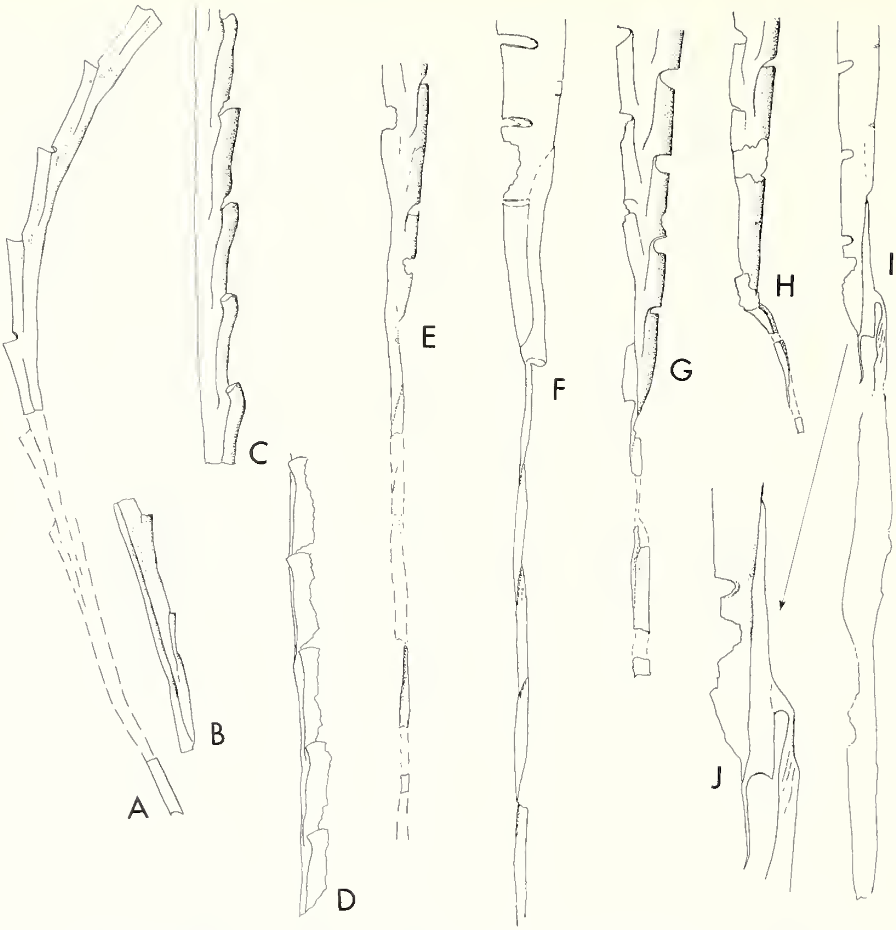
Text-figure 6A–D

1972 *Pseudoglyptograptus* sp. 2; Rickards, p. 278, text-fig. 3.2.

Derivation of name. After Dr Barrie Rickards, who first recognized this species as a distinct taxon.



TEXT-FIG. 7. *Normalograptus? magnus* (H. Lapworth). A–C, *magnus* Biozone; Tynygraig railway cutting. A, JZ 8458. B, JZ 8264. C, JZ 8317. D–G, *magnus* Biozone; Wye valley section. D, DJ 7740. E–F, DJ 7764. G, DJ 7768. All ×10.



TEXT-FIG. 8. A–B, *Coronograptus* aff. *gregarius minusculus* Obut and Sobolevskaya. *cyphus* Biozone; Wye valley section. A, JZ 9764. B, JZ 9765; part/counterpart. C–D, *Pribylograptus sandersoni* (Lapworth). JZB 779; *acinaces* Biozone; Wye valley section. C, lateral view. D, ventral view. E–J, *Rhaphidograptus toernquisti* (Elles and Wood). *triangulatus* or *magnus* Biozone; Tynygraig railway cutting. E, JZ 8057. F, JZ 8229. G, JZ 8065a. H, JZ 8061. I–J, JZ 8060. All × 10 except J, × 20.

Holotype. JZ 8457 (Text-fig. 6B). The specimen, preserved in part relief, originated from the *magnus* Biozone of the Tynygraig railway cutting, Dyfed, Wales (Text-fig. 1).

Additional material. Eleven other specimens from the type locality; two specimens from the *magnus* Biozone of the Wye valley section (Text-fig. 3); two probable specimens from the *magnus* Biozone section at Ysbyty Ystwyth, Dyfed (Text-fig. 1).

Diagnosis. A moderately sized pseudoglyptograptid, increasing in width from under a millimetre proximally to 2·0 mm distally. Thecae with sharp genicula, concave supragenicular walls and marked lappets proximally which become less pronounced distally. Median septum from the second thecal pair, slightly wavy proximally and straight distally.

Description. Widths proximally are 0·7–0·9 mm, 1·1–1·4 mm (rarely to 1·8 mm) at th5, 1·5–1·8 mm at th10 and 2·0–2·1 mm at th20. 2TRDs are 1·3–1·8 mm proximally, 1·6–1·9 mm at th5–7, 1·9–2·0 mm at th10–12 and 2·0 mm at th20–22. The proximal end seems to be of *Normalograptus* type, with part of the lateral wall of the sicula exposed below th1^2. The sicula is exposed on the obverse side for 0·6 mm, to just below the th1 aperture (Text-fig. 6A). The proximal five or six thecae are sigmoidally curved, with interthecal septa that are convex outwards, a sharp geniculum and a supragenicular wall that has a concave curvature which is most pronounced just below the aperture. Prominent apertural lappets are developed (though these may be more accurately described as embayed lateral apertural margins, the ventral apertural margin apparently being smooth) (Text-fig. 6B–D). Well-preserved material (Text-fig. 6B) shows the dorsal thecal wall extending upwards to form a genicular hood. Distally, the apertural lappets become much less prominent, and the supragenicular walls somewhat less concave. The median septum begins from the second thecal pair on both the obverse and reverse sides. It is slightly wavy adjacent to the second and third thecal pairs, and is straight distally.

Discussion. The material appears conspecific with the *Pseudoglyptograptus* sp. 2 of Rickards (1972), also from the *magnus* Biozone of the Rhayader area, though Rickards' figured specimen is slightly narrower and more densely thecate distally. *Pseudoglyptograptus* sp. nov. of Melchin (1989) from the Cape Phillips Formation of Arctic Canada is also similar and undoubtedly closely related; it is significantly more robust, though, with a width of 1·1 mm proximally and 2·3 mm at th10. It also occurs at higher levels, equivalent to the *leptotheca* and *convolutus* Biozones of the British sequence (Melchin 1989, table 1 and fig. 4). *Pseudoglyptograptus* sp. 1 of Rickards (1972) also resembles the taxon under discussion in general thecal and rhabdosomal characters, but is considerably narrower.

These taxa differ slightly from the type species of *Pseudoglyptograptus*, *P. vas* (Bulman and Rickards, 1968), in having more distinct genicula and more obvious apertural lappets. The former feature, in particular, means that poorly preserved or compressed material resembles comparably-sized species of *Normalograptus* (e.g. *N. normalis*) rather than *Glyptograptus*.

Genus RHAPHIDOGRAPTUS Bulman, 1936

Type species. By original designation, *Climacograptus törnquisti* Elles and Wood, 1906.

Rhaphidograptus toernquisti (Elles and Wood, 1906)

Text-figure 8E–J

Discussion. Most material of *R. toernquisti* is consistent with the detailed descriptions of Hutt (1975) and Bjerreskov (1975). However, one population from a *triangulatus*/*magnus* Biozone interval within the Tynygraig railway cutting (Text-fig. 1) shows considerable variability in virgellar form. Most members of this population (Text-fig. 8E–G) possess a virgella similar to that described by Bjerreskov (1975) – an extended structure, up to 12 mm long, that expands away from the sicula to a width of 0·15–0·25 mm and that is twisted into a more-or-less regular clockwise spiral. Bjerreskov's published electron micrograph (1975, pl. 6D) indicates a roughly triangular cross-section in this structure. One specimen from Tynygraig, however, (Text-fig. 8H) shows a curved, horn-like virgella that is strongly thickened at its contact with the sicula, and growing out at an angle to the axis of the rhabdosome. In another, remarkable specimen (Text-fig. 8I–J), the virgella itself is not elongated, and an analogous, but wider, lanceolate structure grows out from the side of the sicula on its antivirgellar side.

This kind of morphological plasticity is unexpected, and further consideration of such phenomena may provide insight into the developmental and skeleton-building mechanisms of graptolites.

Diplograptids of uncertain generic affinity

Graptolites under this heading include: (i) diplograptids with markedly biform thecae and a proximal end of *Normalograptus* (s.l.) type; *Neodiplograptus* was suggested for these by Legrand (1987), but the name is regarded as a synonym of *Normalograptus* (see above); and (ii) diplograptids with a proximal end of *Normalograptus* (s.l.) type and orthograptid thecae distally. No generic or subgeneric name has yet been proposed for this combination of features.

'*Diplograptus*' aff. *modestus primus* Mikhaylova, 1980

Text-figure 9A–C

Material. Eleven specimens from the Cwmere Formation (?*acuminatus-atavus* biozones) at Lan Goch, northeast of Rhayader, Powys (SO 0169 7019).

Description. The rhabdosome is rapidly expanding. Proximal widths are 0·8–1·1 mm, widths at th5 are 1·4–2·1 mm, 2·2–2·5 mm at th10, and up to 2·6 mm distally. 2TRDs are 1·1–1·2 mm proximally, 1·3–1·4 mm at th5–7, and 1·3–1·5 mm at th10–12. The sicula, seen in one specimen (Text-fig. 9C) is 1·6 mm long, reaching to just above the aperture of th2^2. The proximal end appears to be of *Normalograptus* type (*sensu* Melchin and Mitchell 1991). The thecae are biform. The proximal *c.* five thecal pairs are of broadly amplexograptid aspect (though lacking apertural lappets), with sharp genicula, above which the supragenicular walls are outwardly inclined. Distally, the thecae are orthograptid, with straight ventral walls and apertures roughly perpendicular to the thecal axes.

Discussion. The gross rhabdosome shape and thecal spacing of this taxon are similar to that of '*Diplograptus*' *modestus modestus* Lapworth, 1876. Lapworth's figured type of '*D*'. *m. modestus* is missing (Strachan 1971) and the concept of the species has been taken from Elles and Wood's (1907) redescription, in large part illustrated by material from Lapworth's collection. Re-examination of this (?topotype) material has shown that thecae throughout the rhabdosome are essentially uniform, having concave infragenicular walls separated from straight, outward leaning supragenicular walls by distinct genicula; this appears to be a primary feature and not the result of differential compaction following stipe torsion. Thus the material from central Wales is probably not closely related to '*D*'. *m. modestus* (*sensu* Elles and Wood). In its strongly biform nature it resembles '*D*'. *modestus primus* Mikhaylova from the *acuminatus* Biozone of Kazakhstan (figured in Koren' *et al.* 1980) which is narrower, most specimens not exceeding 1·7 mm in width.

'*Orthograptus*' *cabanensis* sp. nov.

Text-figure 9I–L

Derivation of name. After Caban coch reservoir, by which the type locality is sited.

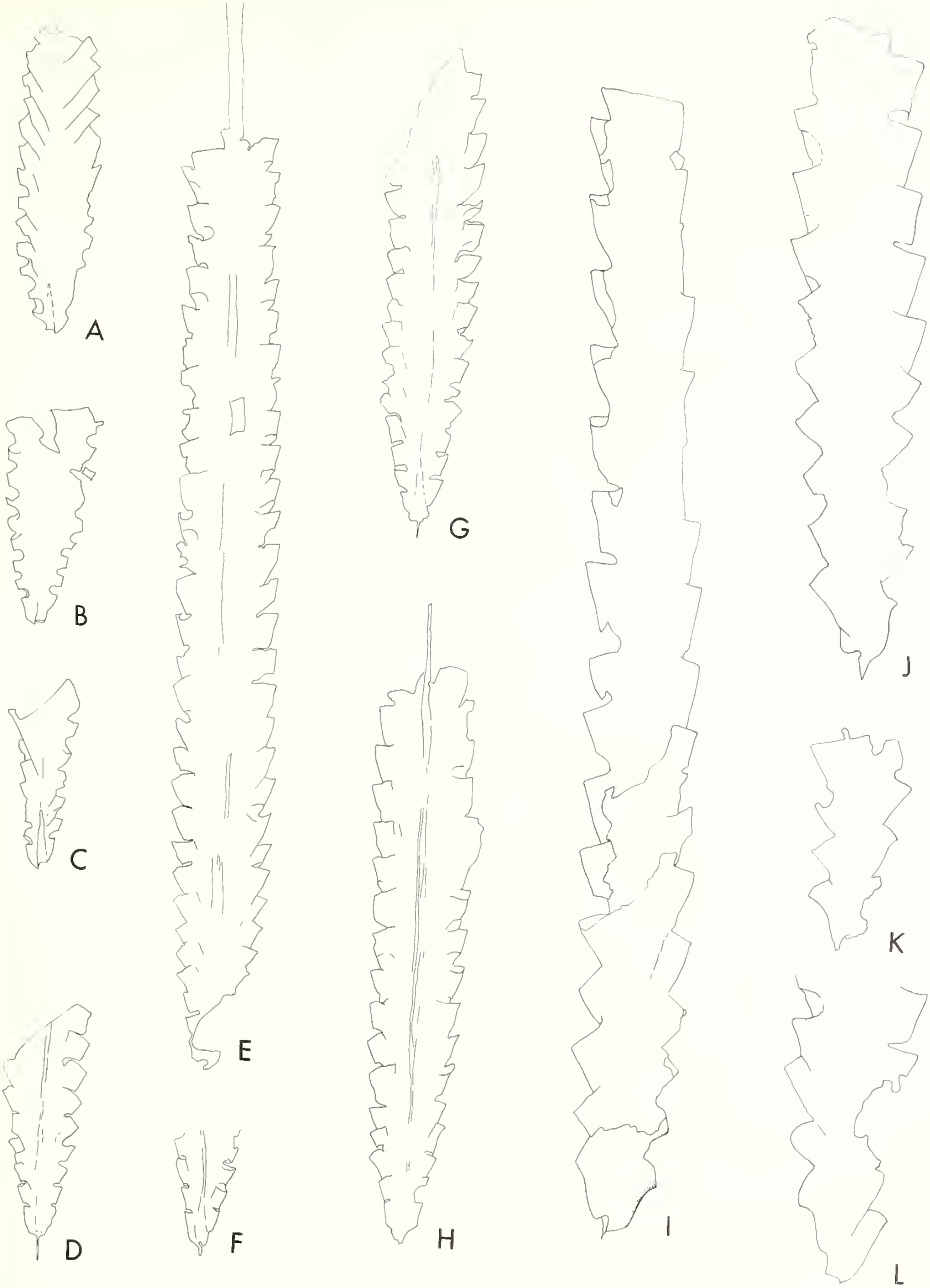
Holotype. DJ 8991 (Text-fig. 9J), preserved in slight relief, and originating from the Cwmere Formation (upper *acuminatus* Biozone) of the Craig Fawr track section (SN 9194 6296) (Text-fig. 1).

Additional material. Seventeen other specimens from the type section (Text-fig. 1); one specimen from a nearby stream section (*c.* SN 9242 6370).

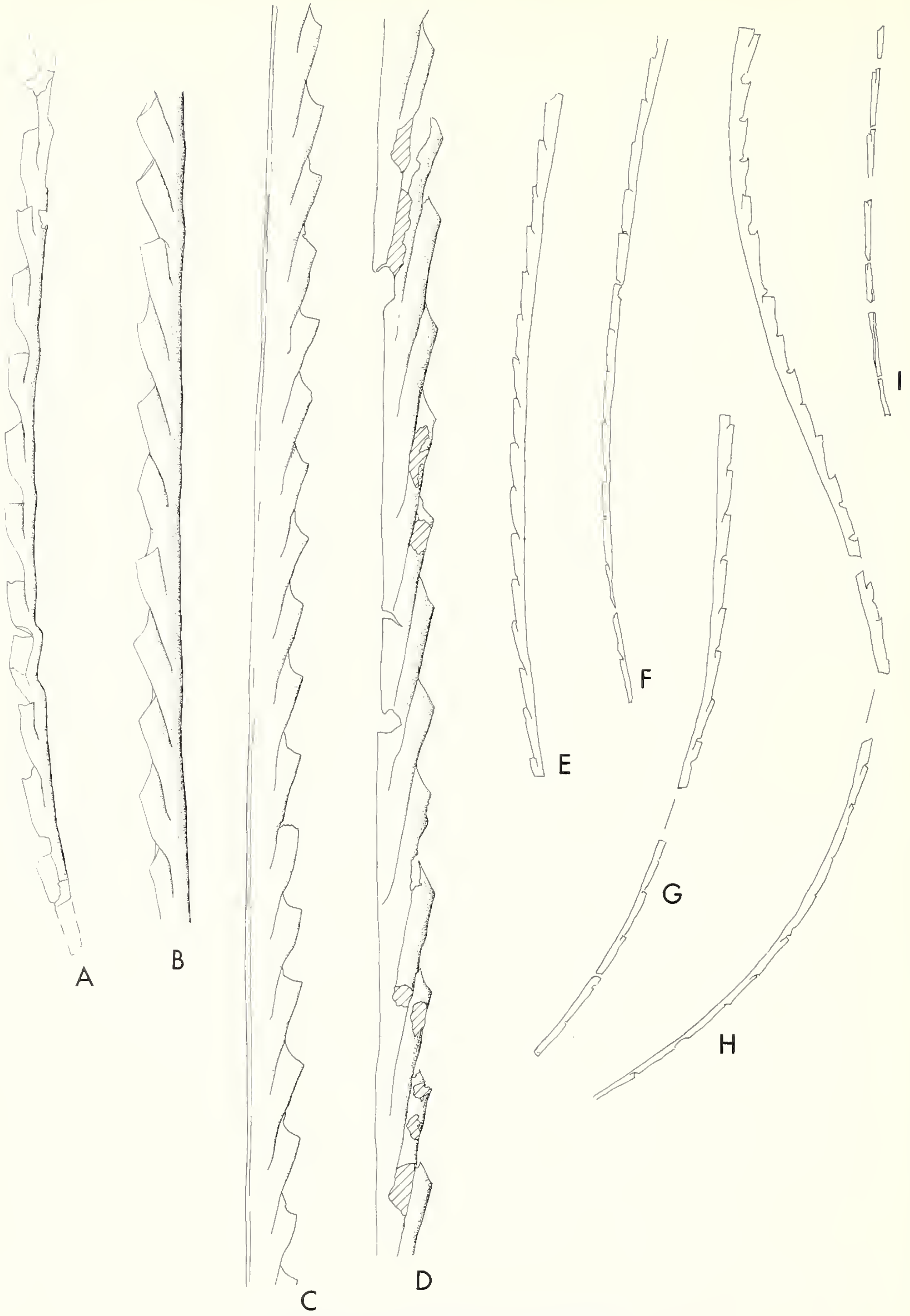
Diagnosis. A graptolite with a relatively wide proximal end of *Normalograptus* type, th1^1 and 1^2 that are everted, and orthograptid thecae subsequently.

Description. Widths are 1·2–1·35 mm at the first thecal pair, 1·7–1·85 mm at the fifth, and 1·7–2·0 mm at the tenth. 2TRDs are 1·55–1·7 mm proximally, 1·8–2·0 mm at th5–7 and 2·2 mm at th10–12. The proximal end appears to be of *Normalograptus* (s.l.) type (*sensu* Melchin and Mitchell 1991), with *c.* 0·3 mm of the sicula wall free below th1^2, and a convex curvature to the proximal ventral walls of th1^1 and 1^2. However, the ventral thecal walls of th1^1 and 1^2 are distinctive in being concavely curved below the apertures, which are everted and appear convex in outline. Distally, thecae appear basically orthograptid, though traces of genicula (possibly compactional artefacts) are visible in some orientations; the apertures also partly 'enclose' the ventral walls of succeeding thecae. Details of the sicula and median septum were not apparent.

Discussion. This species closely resembles the *Orthograptus* sp. nov. of Melchin (1989, fig. 6E–F) from the *atavus* Biozone of Arctic Canada. That species has a narrower proximal end, though, and the apertural portions of th1^1 and 1^2 appear simple, not everted. These differences are also shared by *Gl.* aff. *nanus* Mu and Ni from the *acuminatus* Biozone of Arctic Canada (Melchin 1989, Fig. 5E),



TEXT-FIG. 9. A–C, '*Diplograptus*' aff. *modestus primus* Mikhaylova. Probably *acuminatus* Biozone; Lan Goch; ×5. A, JZ 4666. B, JZ 4660. C, JZ 4662. D–H, *Diplograptus modestus modestus* Lapworth. BU 1292; *atavus* Biozone of Dob's Linn, Scotland; ×5. I–L, '*Orthograptus*' *cabanensis* sp. nov. Upper *acuminatus* Biozone; ×10. I, JZ 2575; Craig Fawr track section. J, DJ 8991, holotype; Craig Fawr track section. K, DJ 8991; Craig Fawr track section. L, DJ 9106; stream by Elan village.



TEXT-FIG. 10. For legend see facing page.

which is also narrower and more densely thecate distally. *Orthograptus illustris* Koren' and Mikhaylova, 1980 from the *acuminatus* Biozone of Kazakhstan (Koren' *et al.* 1980, p. 158) and *Diplograptus* aff. *parvulus* (H. Lapworth, 1900) figured by Štorch (1983, pl. 4, fig. 4; text-fig. 20) from the *ascensus* and *acuminatus* Biozones of Bohemia are further generally comparable, but are smaller and more densely thecate, with simple th1^1 and 1^2.

The '*Orthograptus truncatus abbreviatus*' figured by Hutt (1974, p. 33, pl. 8, figs 9–10; text-fig. 8, fig. 9) from the *acuminatus* Biozone of the Lake District may also be related. *O. truncatus abbreviatus s.s.* is an Upper Ordovician taxon within the *amplexicaule* group of *Orthograptus* (*sensu* Mitchell (1987)), possessing Mitchell's pattern G astogeny. This group reportedly became extinct during the end-Ordovician glaciation (Melchin and Mitchell 1991). The material figured by Hutt is not well-preserved proximally, but possesses a pointed proximal end more reminiscent of *Normalograptus* than of *Orthograptus* and the single proximal thecal spine figured (Hutt 1974, text-fig. 8, fig. 9) may be a preservational feature. In rhabdosome dimensions, it most resembles *Orthograptus* sp. nov. of Melchin (1989).

This group of 'orthograptids', taken as a whole, appears to be stratigraphically useful, seemingly being confined to the *acuminatus* and *atavus* biozones worldwide. The proximal end, with its initial rounding, contrasts with that of later 'orthograptids' (e.g. '*O.*' *insectiformis* and '*O.*' *cyperoides*) where the earliest visible portions of th1^1 and 1^2 are straight, giving a V-shaped outline.

cf. '*Orthograptus*' *mutabilis* Elles and Wood, 1907

Text-figure 6G

cf. 1907 *Orthograptus mutabilis* Elles and Wood, p. 232, pl. 29, fig. 1*a–c*; ?*non* d; text-fig. 153*a–c*.
non 1974 *Orthograptus* aff. *mutabilis* Elles and Wood; Hutt, p. 33, pl. 16, fig. 6; text-fig. 8, fig. 10.

Material. Two probable distal fragments from the *acinaces* Biozone of the Wye valley section (Text-fig. 3); one proximal end from the *cyphus* Biozone of the same section.

Discussion. The single, well-preserved proximal end compares well with the type material, though is also indistinguishable from the proximal parts of early petalograptids (e.g. *P. minor*, *P. ovatoelongatus*), which have been recorded from the succeeding *triangulatus* Biozone in Britain (Hutt 1975; Rickards 1976). The *cyphus* Biozone record of *P. minor* in Germany (Schauer 1971) may also represent this taxon. A close evolutionary connection between '*O.*' *mutabilis* and the petalograptids is highly probable. The stratigraphically younger '*O.*' aff. *mutabilis* of Hutt (1974) is significantly different and may not be closely related; its proximal end is much narrower and the ventral margins of th1^1 and 1^2 are straight, rather than concavely curved.

Genus ATAVOGRAPTUS Rickards, 1974

Type species. By original designation of Rickards 1974, p. 141; *Monograptus atavus* Jones, 1909.

cf. *Atavograptus atavus* (Jones, 1909)

Text-figure 10C

Discussion. Three distal fragments from the *cyphus* Biozone of the Wye valley section (Text-fig. 3) are notable for their poorly defined genicula and marked eversion of the thecal apertures (Text-fig. 10C). In this they differ from 'typical' *atavus* (Text-fig. 10A), though some material from Jones' type

TEXT-FIG. 10. A–B, *Atavograptus atavus* (Jones). ?*atavus* Biozone; Rheidol Gorge. A, GSM 23710, lectotype. B, Pg 991, Jones Coll. C, cf. *Atavograptus atavus* (Jones). JZ 9775; *cyphus* Biozone; Wye valley section. D, *Monograptus* sp. 1. JZ 9847; *triangulatus* Biozone; Wye valley section. E–I, *Atavograptus gracilis* Hutt. *atavus* Biozone; Wye valley section. E, JZ 9401. F, JZ 9413. G, JZ 9431. H, JZ 9438. I, DJ 8836. A–D ×10, E–I ×5.

collection shows comparable features (Text-fig. 10B). The material also may be closely related to *Monograptus* sp. 1, from the *triangulatus* Biozone of the Wye valley (Text-fig. 10D; see below), which differs in having even more markedly everted thecal apertures and a greater amount of thecal overlap.

Atavograptus gracilis Hutt, 1975

Text-figure 10E–I

1970 *Monograptus* sp. 2, Hutt and Rickards, p. 76, text-fig. 3*e–f*.
1974 *Monograptus* sp. nov. A, Hutt, p. 6.
1975 *Atavograptus gracilis* Hutt, p. 63, pl. 14, fig. 4; text-fig. 14, fig. 4.
non 1982 *Atavograptus gracilis* Hutt; Lenz, p. 48, figs 4A–B, L, 19H–I.

Holotype. SM A60417, from the *atavus* Biozone of School Beck, Lake District, England.

Material. Over twenty fragmentary specimens, preserved in slight relief, from the *atavus* Biozone of the Wye valley section (Text-fig. 2), including one proximal end probably belonging to this species.

Revised diagnosis. Long, slender, gently curved rhabdosome (normally dorsally, rarely ventrally). Maximum width 0·8 mm, usually 0·5–0·6 mm. Probably long, slender sicula. Overlap increases, thecal spacing decreases, distally. Proximal and mesial thecae with fairly sharp genicula and small apertures, distal thecae with more flowing genicula.

Description. A single proximal end, probably referable to this species, has been found (Text-fig. 10I). The sicula is 3·8 mm long and 0·2 mm wide at its base. Th1 originates 1·4 mm from its base, its aperture being 0·7 mm above the sicula apex. Dorso-ventral width varies from 0·175 mm at th1 to 0·225 mm at th4, the 2TRD proximally being 4·0 mm. Overlap proximally is one-eighth. More distal fragments range in width from *c*. 0·2 to 0·5 mm, rarely to 0·6 mm, the increase in width being attained slowly. Most fragments have a gentle dorsal curve, one longer fragment having a moderate ventral curve distally. Thecae are more widely spaced proximally (2TRD *c*. 3·0 mm) than distally (2TRD 2·2–2·5 mm). Overlap increases distally from about one-fifth to one-quarter. Apertures seem simple, and approximately perpendicular to the thecal axis, but they can appear either slightly everted or slightly introverted in different preservational modes. Genicula are present throughout, appearing sharper proximally.

Discussion. Hutt's (1974) material appears conspecific, though attaining somewhat greater maximum widths (to 0·8 mm). The type material was not well enough preserved to show details of the sicula or of the variation in thecal spacing and overlap distally noted here. Lenz's (1982) material ascribed to *A*. cf. *gracilis* is not conspecific, having greater overlap, a shorter sicula, and a more robust proximal portion. *A. gracilis* may be distinguished from *A. atavus* by its narrower rhabdosome, smaller amount of overlap and widely spaced proximal thecae.

The proximal end (Text-fig. 10I), with its long, slender sicula (in contrast to the short sicula of *A. atavus*) suggests a link with *Coronograptus* or *Lagarograptus*.

Genus PRIBYLOGRAPTUS Obut and Sobolevskaya, 1966

Type species. By original designation of Obut and Sobolevskaya (1966, p. 33) *Monograptus incommodus* Törnquist, 1899.

Pribylograptus sandersoni (Lapworth, 1876)

Text-figure 8C–D

1876 *Monograptus Sandersoni* Lapworth, p. 320, pl. 11, fig. 2*a–e*.
1911 *Monograptus Sandersoni* Lapworth; Elles and Wood, p. 404, pl. 39, fig. 10*a–e*; text-fig. 271*a–d*.
1970 *Pribylograptus sandersoni* (Lapworth); Hutt and Rickards, text-fig. 2*b*.
1970 *Monograptus sandersoni* Lapworth; Rickards, p. 66, text-fig. 14, fig. 25.

Lectotype. Specimen (not yet recognized: see Strachan 1971, p. 60) figured by Lapworth (1876, pl. 11, fig. 2*a*), selected by Přibyl (1948).

Material. Three distal fragments, in relief, from the *acinaces* Biozone of the Wye valley section (Text-fig. 3).

Description. The best-preserved fragment has a dorso-ventral width of 0·6 mm and a 2TRD of 2·4 mm. The thecae are gently sigmoidally curved, the most marked, convex, curvature occurring just below the aperture. The apertures are moderately laterally expanded, but otherwise essentially simple, without the development of horns or lappets; they are slightly introverted.

Discussion. This material clearly allows the inference (made by Rickards 1970) of the transitional nature of this species between (probably) *Atavograptus* and 'typical' *Pribylograptus* which possesses distinct lateral horns (Rickards and Rushton 1968). These lateral horns appear to be genuine features and not artefacts of interpretation as stated by Loydell (1991).

Monograptus s.l. sp. 1

Text-figure 10D

Material. Ten distal fragments, in partial to full relief, from the *triangulatus* Biozone of the Wye valley section (Text-fig. 3).

Description. The distal stipe fragments are up to 70 mm long. These are approximately straight, or possess a very slight ventral curvature. Widths range from 0·6 mm to 1·2 mm, and 2TRDs range from 2·1 mm to 2·5 mm (rarely to 2·8 mm). Thecae are long straight tubes, inclined at *c*. 15° to the rhabdosome axis, overlapping by just over a half in the most proximal fragment to two-thirds or just over in most fragments. The apertures are markedly everted, slightly concave in outline, and at an angle of *c*. 45° to the thecal axis.

Discussion. This graptolite to some extent resembles *Lagarograptus acinaces* or *Coronograptus cyphus cyphus* in terms of general dimensions and degree of thecal overlap, but differs in having markedly everted apertures. It differs from *Pristiograptus concinnus* in its greater thecal overlap and more markedly everted apertures. It may be related to the cf. *Atavograptus atavus* (described above) from the underlying *cyphus* Biozone.

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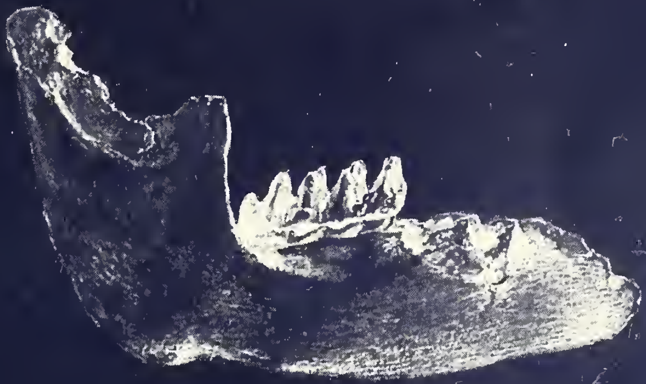

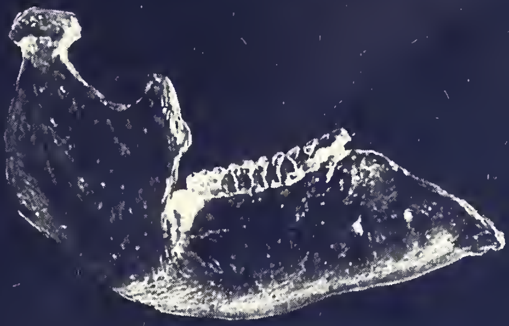

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by H. J. HOFMANN *and* R. H. RAINBIRD

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ABSTRACT. A small assemblage of millimetric black carbonaceous compressions from the Wynniatt Formation of the Shaler Supergroup includes *Chuaria circularis*, *Tawuia dalensis* and *Beltina danai*. Also present are string-like remains that may be either pyritized vendotaeniacean filaments or small burrow fills. The occurrence of *Tawuia* is only the second known from North America. The presence of the *Tawuia–Chuaria* assemblage provides important corroborating evidence for correlation of the Wynniatt Formation of the Minto Inlier with the upper part of the Little Dal Group of the Mackenzie Mountains 1000 km to the southwest.

THE tomaculate carbonaceous megafossil *Tawuia* was first described from the Little Dal Group in the Mackenzie Mountains (Hofmann and Aitken 1979). Many more occurrences have since been discovered in Neoproterozoic sequences. All are from localities in the northern hemisphere, including the latest one from Yakutia (Vidal *et al.* 1993), with the most numerous being in China (Hofmann 1992, fig. 7.3.8.). Until now, the locality in the Mackenzie Mountains was the only one in North America. *Tawuia* is invariably associated with specimens of *Chuaria* and, although the converse is not true, this has led to a working hypothesis of a *Tawuia–Chuaria* assemblage zone with potential chronostratigraphical application (Hofmann 1985). Strata of the Shaler Supergroup on northern Victoria Island were targeted for a specific search for carbonaceous megafossils, because this succession commonly has been correlated with the Mackenzie Mountains Supergroup, based on the similarity of the succession of lithological units (e.g. Aitken *et al.* 1978; Young 1979; 1982, fig. 5; Young *et al.* 1979; Jefferson and Young 1989; Rainbird 1991), as well as on geochronometric constraints (Heaman *et al.* 1992; Rainbird *et al.* 1994*b*). The search for carbonaceous megafossils proved successful when the assemblage was located in the Wynniatt Formation in the Kilian Lake area in July 1993. This new material forms the basis of the following discussion. The sequence also contains abundant and well-preserved organic-walled microfossils, which are under separate study by N. J. Butterfield.

GEOLOGICAL SETTING

The sparse but stratigraphically significant fossil assemblage described herein was obtained from strata of the Shaler Supergroup in the Minto Inlier on Victoria Island, northwestern Canada (Text-figs 1–2). The Minto Inlier is one of several inliers of Shaler Supergroup rocks that collectively comprise the Neoproterozoic Amundsen Basin (Christie *et al.* 1972). The Shaler Supergroup was recently proposed as a consequence of the elevation to formation status of several informal members of the former Shaler Group (Thorsteinsson and Tozer 1962; Rainbird *et al.* 1994*a*). It is generally accepted that sedimentary strata of the Shaler Supergroup belong to Sequence B of Young *et al.* (1979), and are lithostratigraphically equivalent to the Mackenzie Mountains Supergroup in the northern Canadian Cordillera. In the Minto Inlier, the Shaler Supergroup comprises a 4–5 km thick sequence of platform marine carbonate, evaporite, and subordinate siliciclastic rocks and underlying and overlying fluvial and fluvio-deltaic sandstones (Young 1981). It includes, in

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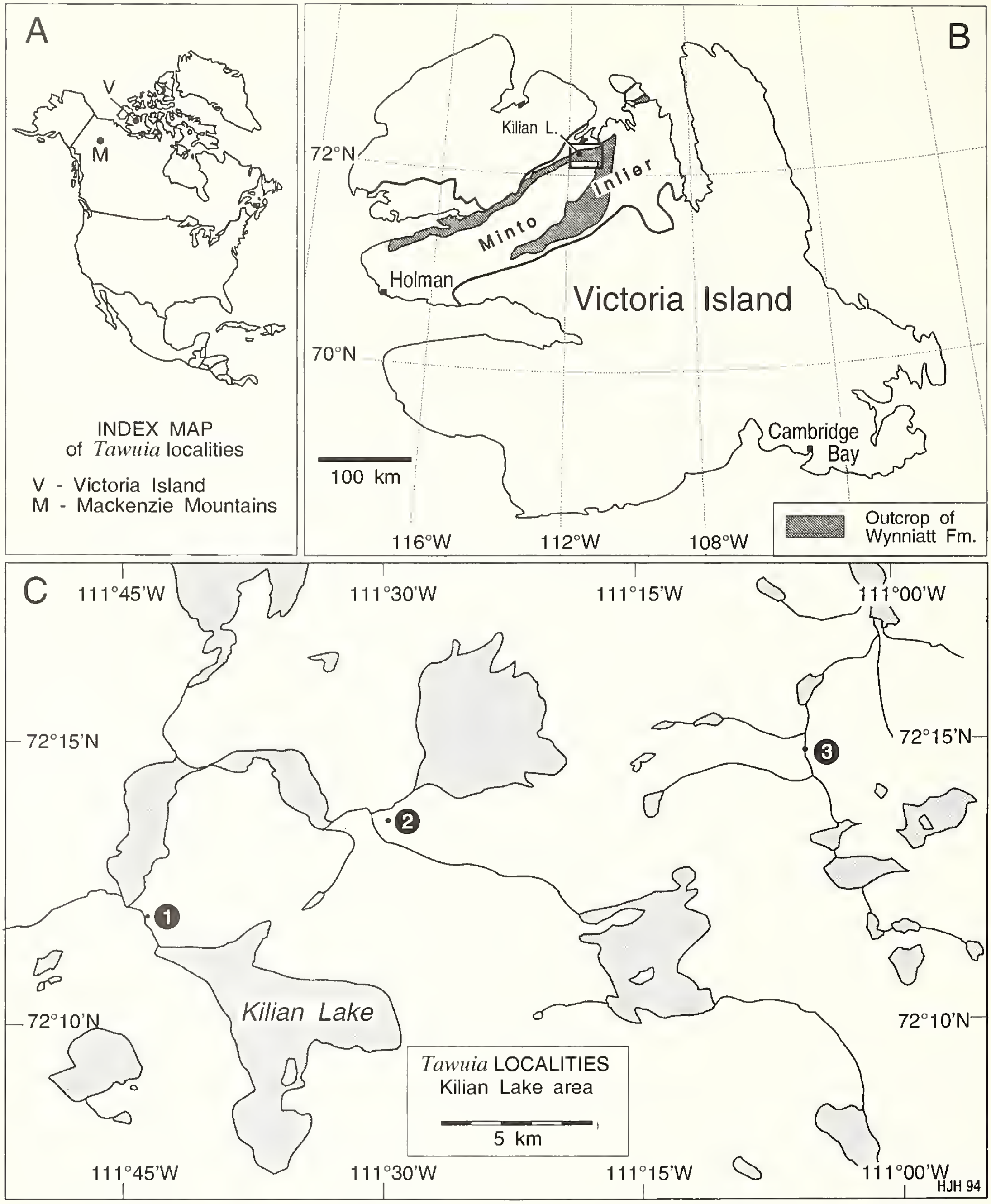
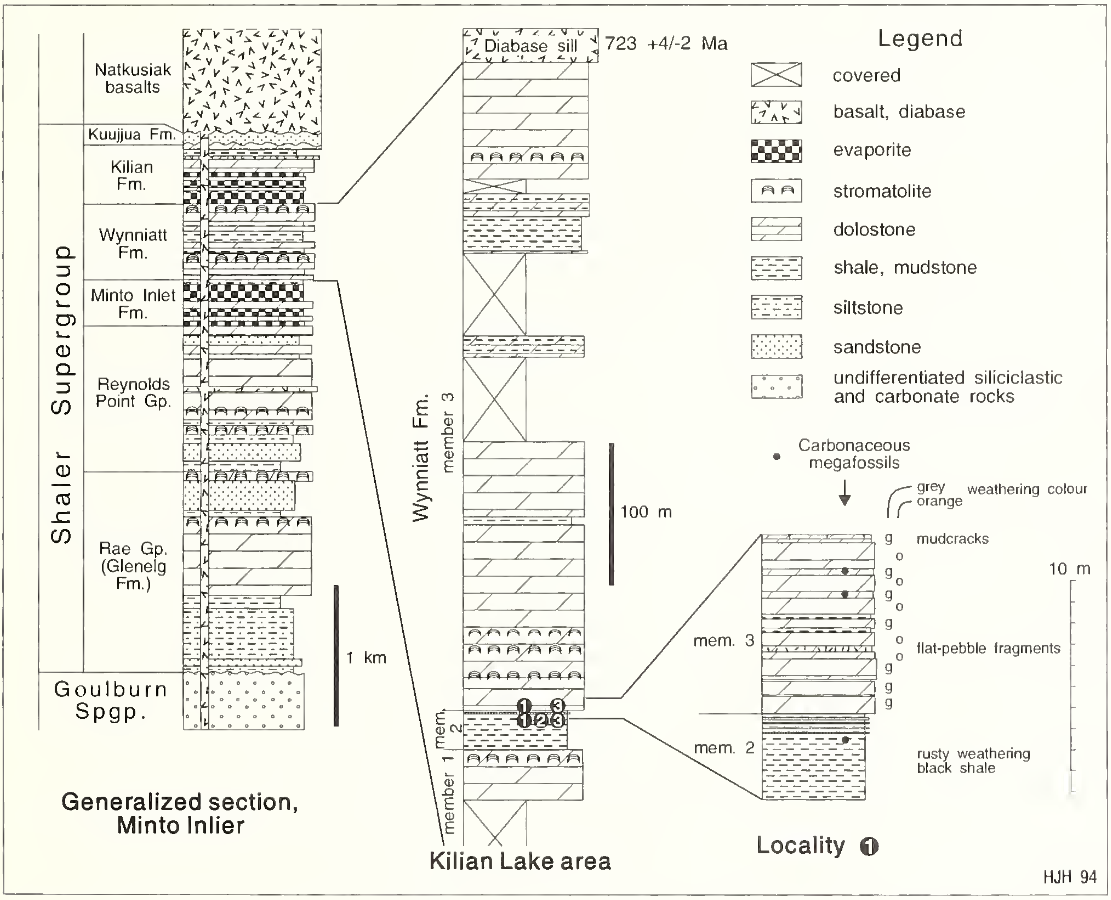


TEXT-FIG. 1. The *Tawuia*-bearing localities. A, map of North America showing Mackenzie Mountains and Victoria Island localities. B, the outcrop belt of the Wynniatt Formation in Minto Inlier, Victoria Island (after Young 1981); rectangle outlines area magnified in C. C, the newly discovered localities in the Kilian Lake area. Geographical coordinates of Locality 1, 72·198° N, 111·728° W; Locality 2, 72·227° N, 111·499° W; Locality 3, 72·247° N, 111·087° W.

ascending stratigraphical order, the Rae Group (formerly Glenelg Formation), Reynolds Point Group, Minto Inlet Formation, Wynniatt Formation, Kilian Formation, and Kuujjua Formation (Thorsteinsson and Tozer 1962; Young 1981; Jefferson 1985; Rainbird 1991; Rainbird *et al.* 1994*a*; Text-fig. 2). The Shaler Supergroup is overlain by the Natkusiak Formation, an up to 1·1 km thick sequence of flood basalt flows and minor volcaniclastic rocks that have been dated at 723 Ma (U–Pb baddeleyite from intrusive equivalents: Heaman *et al.* 1992). A maximum age for the Shaler Supergroup of 1077 Ma has been determined from U–Pb analysis of detrital zircon from the Nelson Head Formation of the Rae Group (Rainbird *et al.* 1994*b*).



TEXT-FIG. 2. Stratigraphical position of the fossils. Section at left after Jefferson and Young (1989, fig. 1; with revised nomenclature of Rainbird *et al.* 1994*a*); section in middle after Young (1981, section K, p. 211), showing positions of Localities 1–3; section at right showing detail of fossil occurrences at Locality 1 at lower end of gorge 1·2 km north-northwest of the outlet of Kilian Lake. Radiometric age from Heaman *et al.* (1992).

The stratigraphical location of the fossil assemblage is just below and above the contact zone between a distinctive rusty black shale member and the overlying grey dolostone member of the Wynniatt Formation (members 2 and 3, respectively, of Rainbird and Young 1989; Text-fig. 2). A relatively rapid shallowing-upward trend is indicated by an abrupt change from primarily flat-laminated carbonaceous mudstone of member 2, indicating deposition below storm wave-base, to the wavy-bedded dolosiltite/dololutite and stromatolitic dolostone of member 3. Episodic subaerial exposure and deposition in the intertidal zone is indicated by desiccation cracks in dolostone interlayers just above the upper fossil-yielding horizon (Text-fig. 2). The depositional environment was influenced by storms in shallow water as indicated by flat-based, wavy-topped quartzarenite beds within the mudstone at the top of member 2, by common intraformational carbonate-pebble conglomerate layers in the lower part of member 3, and by the generally high degree of fragmentation of fossil specimens.

FOSSIL LOCALITIES

The carbonaceous fossils were collected at three localities from near the contact between members 2 and 3 of the Wynniatt Formation, in the northeastern part of the Minto Inlier (Text-figs 1–2). The contact between these two members is relatively sharp and can be readily identified from the air. Locality 1 is situated at the small north-facing cliff, where the contact is exposed on the east side of the lower end of the gorge issuing from Kilian Lake (general area of section H of Young 1981, p. 211). Locality 2 is on the crest of a rusty orange-weathering outcrop with black shale, 8·5 km ENE of Locality 1. Locality 3 exposes the contact zone on both sides of the small stream at the lower end of a gorge 22·5 km ENE of Locality 1.

SYSTEMATIC PALAEONTOLOGY

The specimens here illustrated are deposited in the National Type Fossil Collection of Canada, at the Geological Survey of Canada in Ottawa, and are catalogued under the GSC numbers (109907–109924) cited in the individual figure captions.

Class CHUARIAPHYCEAE Gnilovskaya and Ishchenko *in* Gnilovskaya *et al.*, 1988
Family CHUARIACEAE Wenz, 1938 emend. Duan, 1982
Genus CHUARIA (Walcott) Vidal and Ford, 1985

Type species. Chuaria circularis (Walcott) Vidal and Ford, 1985.

Chuaria circularis (Walcott, 1899) Vidal and Ford, 1985

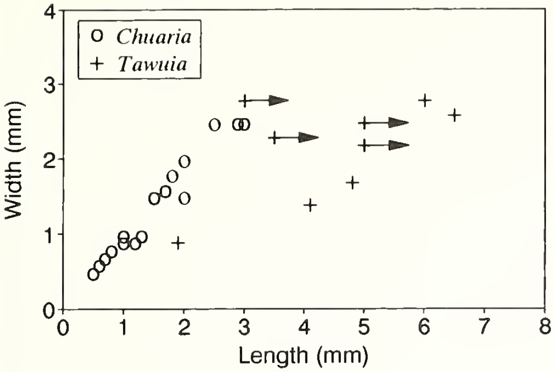
Plate 1, figures 1–6

(For synonymy, see Hofmann 1992, table 23.1.)

Description. Shiny black carbonaceous disks with concentric wrinkling, some with short radial clefts at margin; diameter 0·5–3·0 mm (mean 1·45 mm, $N = 18$) specimens from the black shale member somewhat smaller (mean 1·31, $N = 12$) than those from dolostone member (mean 1·73, $N = 6$); for scatter plot, see Text-figure 3. Some disks slightly elliptical, with aspect ratios of up to 1·3. One specimen with lobate protrusion of shiny black material without wrinkling (Pl. 1, fig. 4).

Occurrence. Localities 1–3.

Remarks. The population density is very low, and only a few specimens are visible even on bedding surfaces of layers on which abundance is greatest. The assemblage is thus relatively poor in



TEXT-FIG. 3. Scatter plot of width versus length of carbonaceous films assigned to *Chuaria* and *Tawuia* from the Wynniatt Formation. Arrows indicate that the original length of the *Tawuia* specimen is greater than the preserved fragment.

macrofossils compared to most other occurrences of the taxon, but it compares with one found in the 'Rusty shale' unit of the Little Dal Group of the Mackenzie Mountains described by Hofmann (1985).

Some specimens are unusual for *Chuaria circularis* in that they show short radial clefts, like those in the much smaller but thick-walled acritarch taxon *Turuchanica* (now considered a species of *Leiosphaeridia*), indicating rupture when the stress during compaction exceeded the tensile strength of the envelope. In one specimen (Pl. 1, fig. 4), rupture apparently has allowed the contents to spill and spread laterally; taphonomic conditions were appropriate for preserving the evidence for this leakage. This feature is uncommon in *Chuaria*, and is thus a noteworthy one for the Wynniatt Formation occurrence.

Family TAWUIACEAE Ishchenko *in* Gnilovskaya *et al.*, 1988
Genus TAWUIA Hofmann *in* Hofmann and Aitken, 1979

Type species. Tawuia dalensis Hofmann *in* Hofmann and Aitken, 1979.

Tawuia dalensis Hofmann *in* Hofmann and Aitken, 1979

Plate 1, figures 7–13

(For synonymy, see Hofmann 1992, table 23.1.)

Description. Short, compressed tomaculate objects, preserved as rectilinear smooth, shiny carbonaceous ribbons with round termini, and as smooth impressions where carbonaceous material is absent and only the form remains; some specimens fragmentary and widely dispersed, population density very low. Observed dimensions for specimens from dolostone 1·9–6·5 mm long, 0·9–2·8 mm wide ($N = 8$), with aspect ratios (length/width) between 1·67 and 2·93; single complete specimen from rusty weathering shale member 1·9 × 0·9 mm (for scatter plot, see Text-fig. 3). Longitudinal and diagonal folds in specimens readily attributable to taphonomic factors.

Occurrence. Localities 1–3.

Remarks. The specimens from the Wynniatt formation are all short, stubby, and straight (no J-, C-, U-, or S-shaped individuals were encountered). In size, shape, and low abundance they most closely resemble the occurrences in the 'Rusty shale unit' of the upper part of the Little Dal Group in the Mackenzie Mountains (Hofmann 1985, pl. 38, figs 2–3). The Wynniatt and Little Dal specimens are indistinguishable from those referred to *Tawuia sinensis* (Duan 1982), which is here considered to be a synonymous taxon.

Class CHUARIAPHYCEAE?
Family BELTINACEAE Hofmann, 1994
Genus BELTINA Walcott, 1899

Type species. Beltina danai Walcott, 1899.

Beltina danai Walcott, 1899

Plate 1, figures 14–17

(For synonymy, see Hofmann 1992, table 23.1.)

Description. Shiny smooth carbonaceous compressions with angulate outlines, as well as smooth impressions where carbonaceous material absent; tendency towards equidimensional polygons, including roughly triangular, quadrate, and more complex polygonal forms. Dimensions ranging from submillimetric, to about 20 mm^2 in area ($N = 6$). Some specimens showing parallel, *en echelon*, cracks perpendicular to marginal crease, or polygonal cracks.

Occurrence. Locality 1.

Remarks. The angulate carbonaceous films are fragments of larger, possibly considerably larger, organisms. The specimen with semicircular outline in Plate 1, figure 16 may be a piece of one of the large taxa known from the Neoproterozoic, such as *Tawuia* or *Longfengshania*, or an as yet undescribed form. The presence of abundant cracks, and the large size, indicate the somewhat brittle nature of the organic material at the time of fossilization, possibly in an advanced stage of dehydration (exposure to air), or material whose physical properties reflect a distinct initial chemical composition. Until larger, more complete specimens become available, the size, nature, and affinities of these remains will stay problematic.

EXPLANATION OF PLATE 1

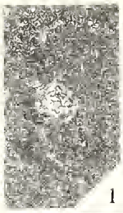
Figs 1–6. *Chuaria circularis* (Walcott) Vidal and Ford; Wynniatt Formation, Neoproterozoic; Victoria Island, Canada. 1, GSC 109907; member 2; Locality 3. 2, GSC 109908; member 2; Locality 1. 3, GSC 109909; member 3; Locality 1. 4, GSC 109910; member 3; Locality 1. 5, GSC 109911; member 2; Locality 2. 6, GSC 109912; member 2; Locality 3.

Figs 7–13. *Tawuia dalensis* Hofmann; Wynniatt Formation, Neoproterozoic; Victoria Island, Canada. 7, GSC 109913; member 2; Locality 2. 8, GSC 109914; member 3; Locality 1. 9, GSC 109915; member 3, Locality 1. 10, GSC 109916; member 3; Locality 1. 11, GSC 109917; member 3; Locality 3. 12, GSC 109918; member 3; Locality 1. 13, GSC 109919; member 3; Locality 3.

Figs 14–17. *Beltina danai* Walcott; Wynniatt Formation, Neoproterozoic; Victoria Island, Canada. 14, GSC 109920; member 3; Locality 1. 15, GSC 109921; member 3; Locality 1. 16, GSC 109922; member 3; Locality 3. 17, GSC 109923; member 3; Locality 1.

Fig. 18. Pyritized vendotaeniacean or burrow; member 3; Wynniatt Formation, Neoproterozoic; Locality 3, Victoria Island, Canada.

All figures are × 10.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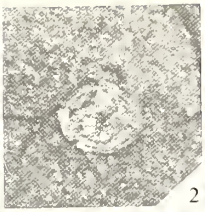
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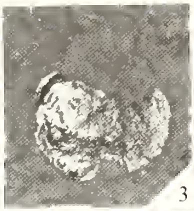
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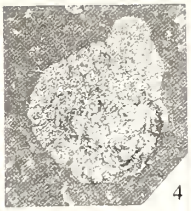
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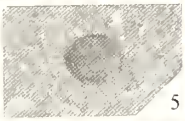
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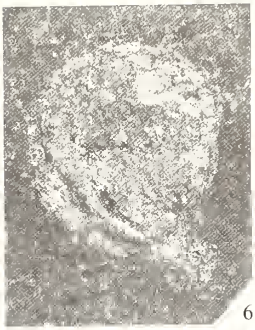
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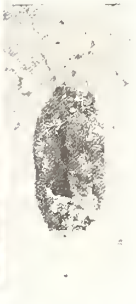
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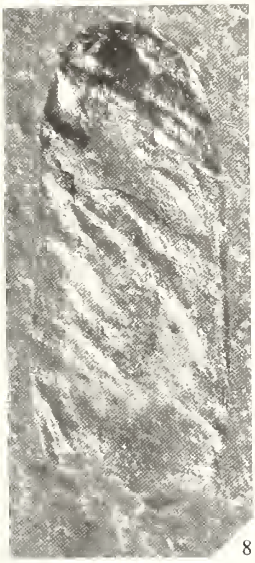
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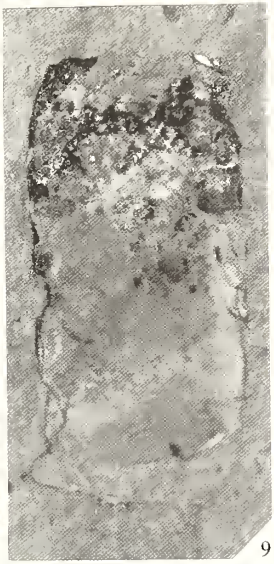
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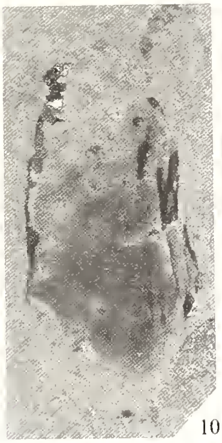
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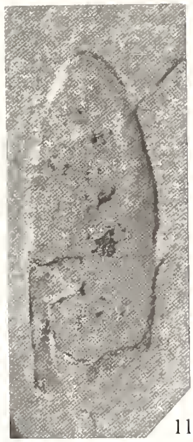
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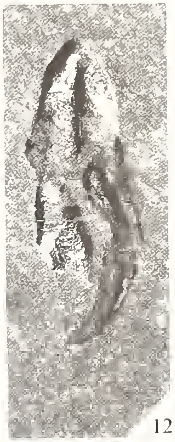
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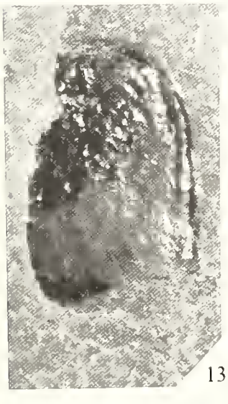
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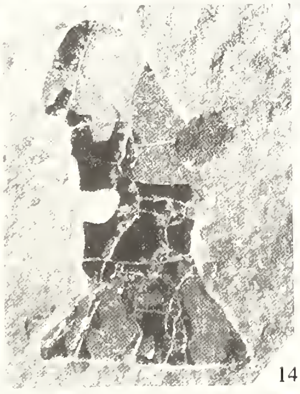
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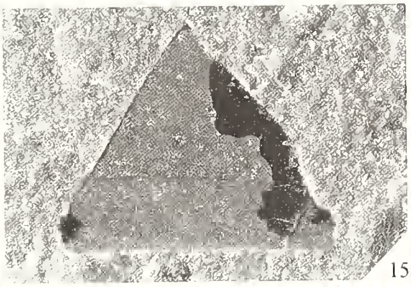
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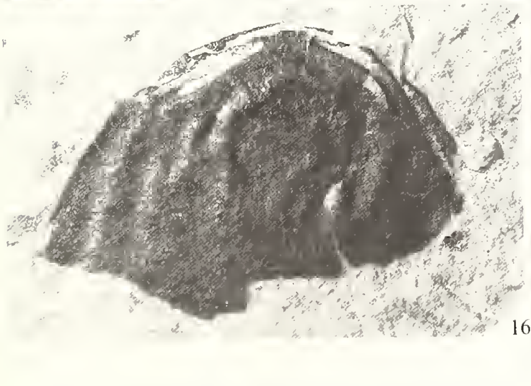
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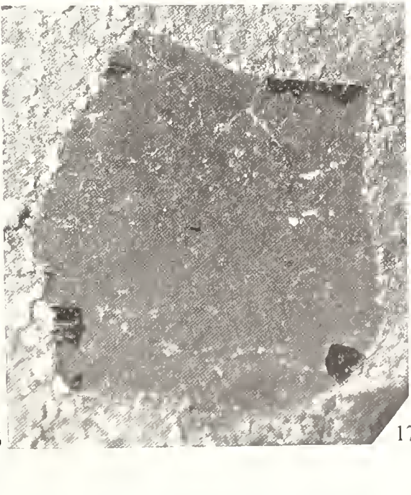
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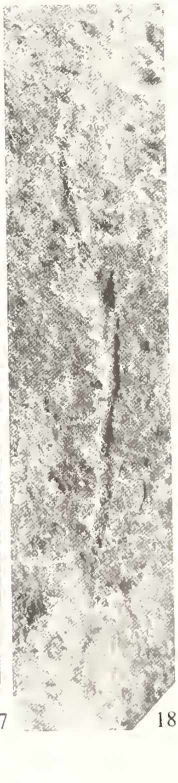
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HOFMANN and RAINBIRD, *Neoproterozoic megafossils*

Other remains
Vendotaeniacean or trace fossil

Plate 1, figure 18

Description. Smooth three-dimensional strings of uniform width, compositionally different from matrix; cross section elliptical, 0·15 mm wide, 0·1 mm high; best preserved fragment, 6·5 mm long, partially pyritized, slightly bent, both part and counterpart preserved; two smaller specimens 1·5 and 1·0 mm long, respectively, both altered to limonite.

Occurrence. Locality 3.

Remarks. The available material is insufficient to do more complete studies without destroying the best preserved specimen. Strings of similar size, but preserved as microcrystalline calcite in dolosiltite, were reported as *Tyrasotaenia*? sp. from the Little Dal Group in the Mackenzie Mountains. As with the Little Dal material, the Wynniatt remains may represent partially pyritized filament casts of vendotaeniaceans such as *Tyrasotaenia*, or tiny, filled, *Planolites*-like burrows. The conservative interpretation, that they represent vendotaeniaceans, is difficult to reconcile with the fact that all the other associated fossils are preserved as carbonaceous compressions rather than three-dimensional objects. An alternative interpretation, previously considered for the strings from the Little Dal Group, is that these fossils may represent fills of tiny burrows of vagile endobionts of unknown affinities, possibly protistan heterotrophs or primitive metazoans (Hofmann 1985, p. 350). However, while the new material could be taken as further circumstantial evidence for the existence of organisms capable of producing trace fossils as far back as the mid-Neoproterozoic, the true nature of the present material remains unresolved.

DISCUSSION

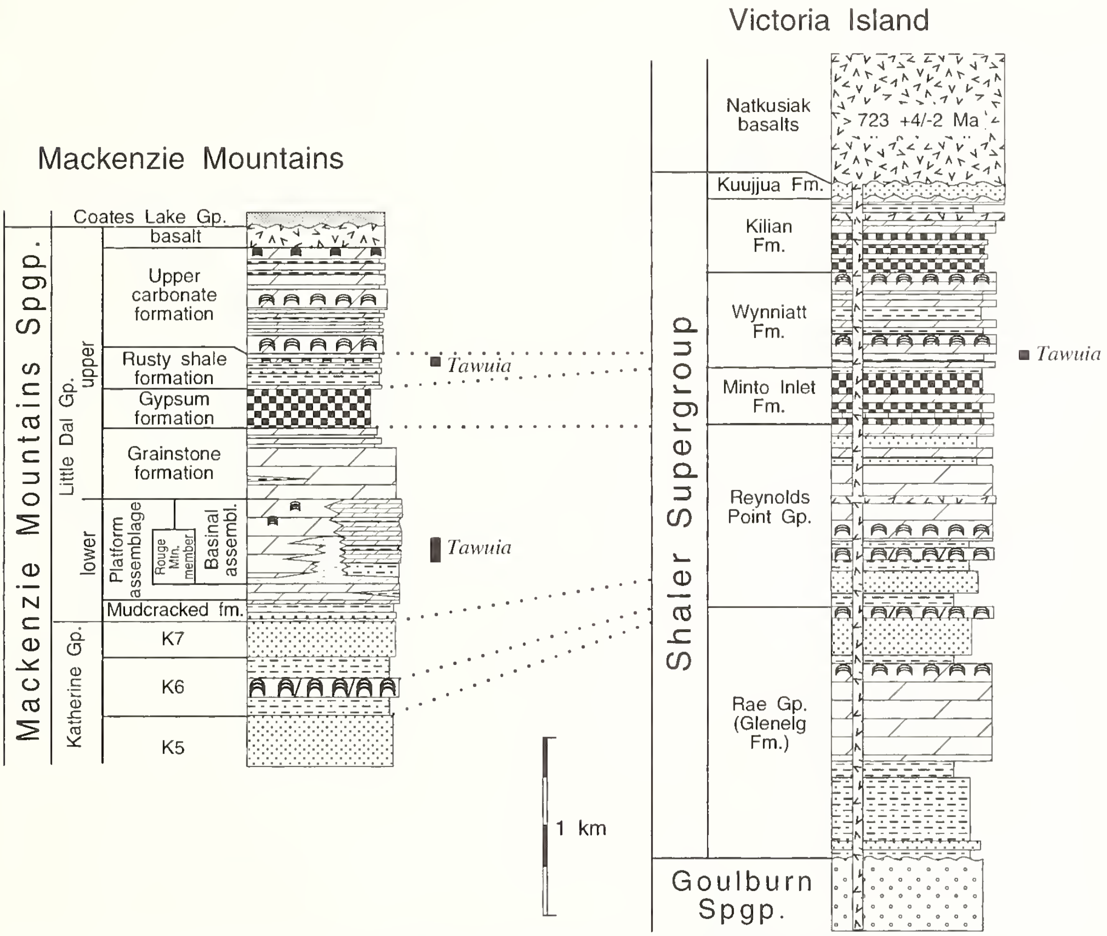
The assemblage of carbonaceous fossils in the Wynniatt Formation is characterized by low abundance; specimens are small, dispersed, and commonly fragmentary. The angular and isolated nature of films assigned to *Beltina* demonstrate that probably they were reworked in a high energy environment. Moreover, the presence of desiccation cracks in dolosiltite within a few decimeters of the *Tawuia*-bearing layers at Locality 1 indicates episodic emergence and, at most, intertidal water depths during the accumulation of this material.

Early-formed taphonomic features such as concentric folds in *Chuaria*, and diagonal, *en echelon*, folds in *Tawuia*, and marginal creases in *Beltina* specimens show the pliable nature of the fossil materials at the time of deposition. Parallel and triradiate shrinkage cracks in the thicker angulate films demonstrate increasing brittleness of the films with maturation of the organic matter during diagenesis. Similar cracking of carbonaceous residue was observed in *Tawuia* specimens in the Little Dal Group (Hofmann 1985, pl. 37, fig. 5). The presence of radial clefts in some *Chuaria* specimens and lobate pattern of spilled cell contents of one specimen are significant features of this assemblage.

The carbonaceous fossils in the Wynniatt Formation are comparable to those in the Little Dal Group of the Mackenzie Mountains, but the assemblage is much more depauperate. In particular, in their small size and sparse population density the remains more closely resemble those in the 'Rusty shale' unit in the upper Little Dal Group than those in the 'Basinal' and 'Platformal' assemblages in the lower Little Dal Group, which have abundant and very large specimens (Hofmann 1985, p. 333). The balloon-shaped *Longfengshania*, the coiled filament *Grypania*, and the questionably branched filamentous *Daltaenia* were not encountered in the Wynniatt Formation. However, these latter taxa are very rare in the Little Dal group, and their apparent absence in the Wynniatt biota may simply reflect the much lower fossil abundance there, or may be due to differing palaeoenvironmental settings.

The presence of a new occurrence of three-dimensionally preserved strings of sub-millimetric diameter in the Wynniatt Formation contributes more circumstantial, though inconclusive, evidence for burrowing activity of microscopic organisms in sediments predating late Neoproterozoic glaciations.

The correlation of the Victoria Island and Mackenzie Mountains sections, incorporating the new biota from the lower part of the Wynniatt Formation, is shown in Text-figure 4. The carbonaceous megafossils support the scheme proposed by Young (1979, table 1, but not fig. 1, which is different because in that figure the 'Rusty shale' unit is correlated with the Minto Inlet Formation); his later paper (Young 1982, fig. 5) also shows the correlation now preferred.



TEXT-FIG. 4. Correlation of *Tawuia–Chuaria* assemblages in the Mackenzie Mountains (stratigraphy after Aitken 1981) and in Victoria Island (stratigraphy after Rainbird *et al.* 1994*a*).

CONCLUSIONS

The new carbonaceous macrobiota demonstrates the presence of *Tawuia*, *Chuaria*, and *Beltina* in the Wynniatt Formation on Victoria Island, only the second area in North America from which *Tawuia* is now known. The occurrence is consistent with the concept of a broad Neoproterozoic *Tawuia–Chuaria* biozone, and it reinforces long-distance correlation of the Shaler Supergroup with the Mackenzie Mountains Supergroup. The data indicate that representatives of the *Tawuia–Chuaria* assemblage of the lower part of the Little Dal Group should be looked for in the Reynolds Point Group.

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THE STATUS OF THE SAUROPTERYGIAN REPTILE *NOTHOSAURUS JUVENILIS* FROM THE MIDDLE TRIASSIC OF GERMANY

by OLIVIER RIEPPEL

ABSTRACT. The holotype and only known specimen of *Nothosaurus juvenilis* from the Hauptmuschelkalk of Germany is redescribed and compared with the type material of all other *Nothosaurus* species described from the Muschelkalk of central Europe. *N. juvenilis* proves to be a valid species diagnosed by morphological features and by cranial proportions, as well as by its small overall size. It overlaps in stratigraphical and geographical distribution with a medium-sized and a large species of the genus *Nothosaurus*, and thus provides the first evidence for niche partitioning among coexisting species of that genus.

NOTHOSAURUS juvenilis was first described by Edinger (1921*a*) in her unpublished Ph.D. thesis. The specimen was collected by R. H. M. König (1862–1921) from the Hauptmuschelkalk (Lower Trochitenkalk, mo1) in the Nusslocher Quarry along the road to Wiesloch near Heidelberg, Germany. Edinger (1921*a*, p. 47) described the skull as *Nothosaurus juvenilis* n. sp., but voiced concern that the specimen might represent a juvenile individual of *Nothosaurus mirabilis*. She asserted that if the status of *N. juvenilis* as a separate species was eventually corroborated, it should be re-named *N. koenigi*, honouring the collector of the fossil. In the same year, Edinger (1921*b*, fig. 4) published an excerpt of her thesis, in which she figured the anterior part of the palate of the specimen; in the figure caption, she referred to the specimen as *Nothosaurus juvenilis* sp. nov., without any further comment. No diagnosis was given for this new species. Her drawing of the palate of *N. juvenilis* was reproduced by Edmund (1960, fig. 11; 1969, fig. 51) in his discussion of tooth replacement in sauropterygians.

The photographs of *Nothosaurus juvenilis* published by Edinger (1921*a*) were reproduced by Haas (1963), who compared the specimen with *Micronothosaurus stensiöi* Haas, a partial skull from Israel (probably referable to *Cymatosaurus* – Schultze 1970) but offered no further statements on the taxonomic status of the specimen. Schultze (1970) redescribed the skull of a small nothosaur from the Lettenkeuper first mentioned by Edinger (1922), designating it the holotype of a new species, *Nothosaurus edingerae*. In so doing, he reviewed the synonymy of nothosaur species on the basis of published descriptions, indicating that a critical review of nothosaur systematics would have to be based on an examination of the original material (Schultze 1970, footnote 1 on p. 218). Nevertheless, Schultze (1970, pp. 225–226) provided the first diagnosis of *N. juvenilis*, arguing that the specimen should be considered a separate species rather than a juvenile specimen of a species already known.

The purpose of this paper is to redescribe the holotype of *Nothosaurus juvenilis* Edinger as preserved today, to corroborate its status as a separate species, and to diagnose it on the basis of homology (synapomorphy, autapomorphy) in comparison with other species of *Nothosaurus* from the Muschelkalk of central Europe (see Appendix for list of comparative material), particularly *N. mirabilis* and *N.* '*münsteri*' (the latter species is generally thought to be represented by juvenile *Nothosaurus mirabilis* specimens – Edinger 1921*a*; Schultze 1970; Kruckow 1979). This is part of a research programme designed to identify the terminal taxa (species) within the genus *Nothosaurus* on an unambiguous basis (Rieppel and Wild 1994). The assessment of the phylogenetic relationships of *Nothosaurus juvenilis* will have to await the review of the status of other *Nothosaurus* species

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described to date. The diagnosis of the genus *Nothosaurus* will remain problematical until a better knowledge of the terminal taxa is attained.

SYSTEMATIC PALAEONTOLOGY

Order SAUROPTERYGIA Owen, 1860
Suborder EUSAUROPTERYGIA Tschanz, 1989
Family NOTHOSAURIDAE Baur, 1889
Genus NOTHOSAURUS Münster, 1834

Type species. Nothosaurus mirabilis Münster, 1834, from the Upper Muschelkalk, Middle Triassic, of Germany.

Diagnosis. Medium-sized to large eusauropterygians with a longirostrine skull, constricted snout, large and elongated upper temporal fossae, posteriorly displaced pineal foramen, paired fangs in the maxilla, enlarged fangs in the posterior symphyseal area of lower jaw, lower jaw symphysis distinctly elongated and distinctly set off from lower jaw ramus, vertebrae platycoelous and non-notochordal with short and stout transverse processes.

Distribution. Triassic (Anisian to uppermost Carnian) of Europe and Asia.

Nothosaurus juvenilis Edinger, 1921*b*

Text-figures 1–3, 7A

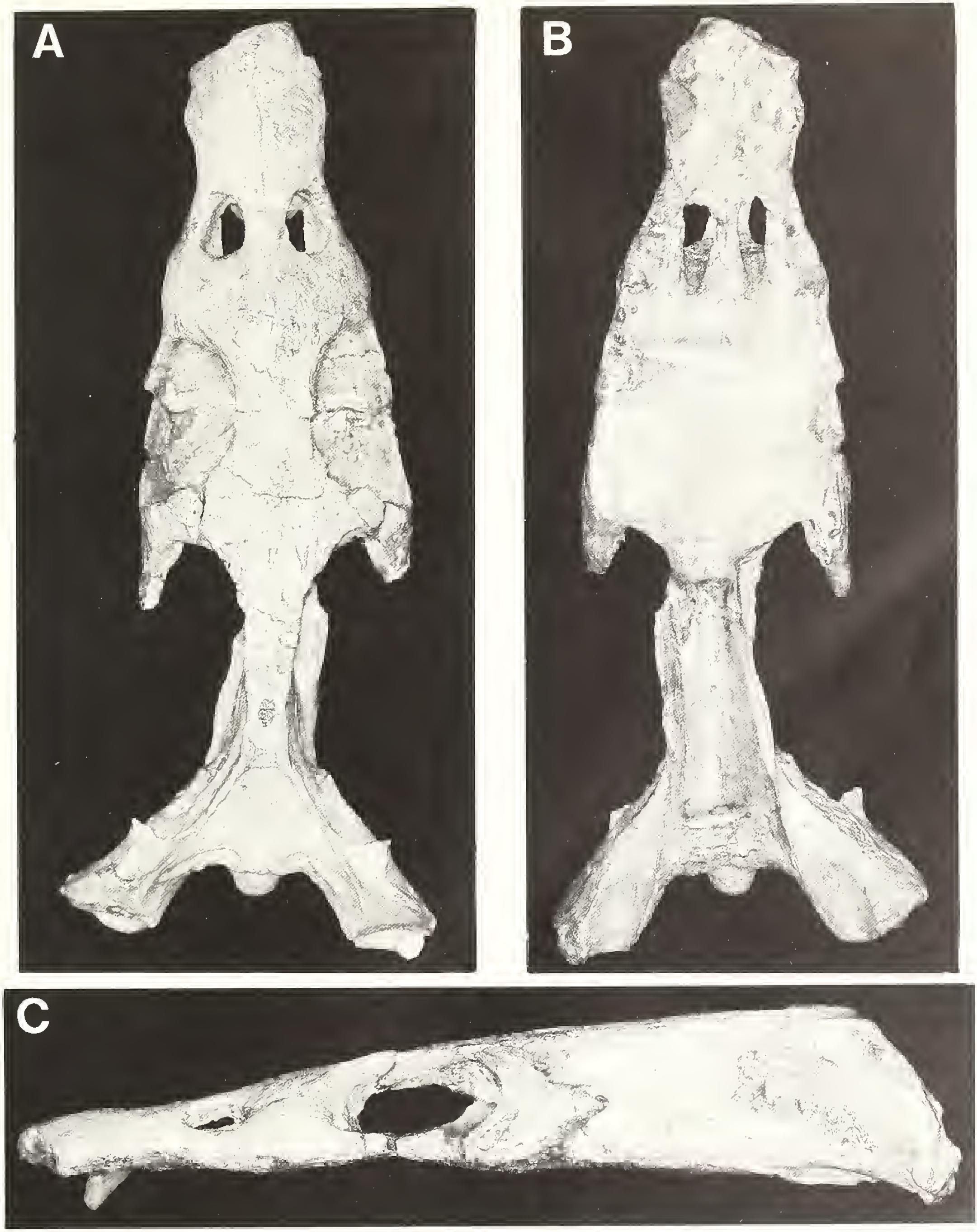
1921*a*	*Nothosaurus juvenilis* Edinger, p. 47, figs 8–11 [unpublished].
1921*b*	*Nothosaurus juvenilis* Edinger, fig. 4.
1963	*Nothosaurus juvenilis* Edinger; Haas, p. 37, pl. 12.
1970	*Nothosaurus juvenilis* Edinger; Schultze, p. 225, fig. 13.

Holotype. The holotype and only known specimen (Text-fig. 1) is kept at the Palaeontological and Geological Institute and Museum, University of Heidelberg (König Collection, K.8698–1).

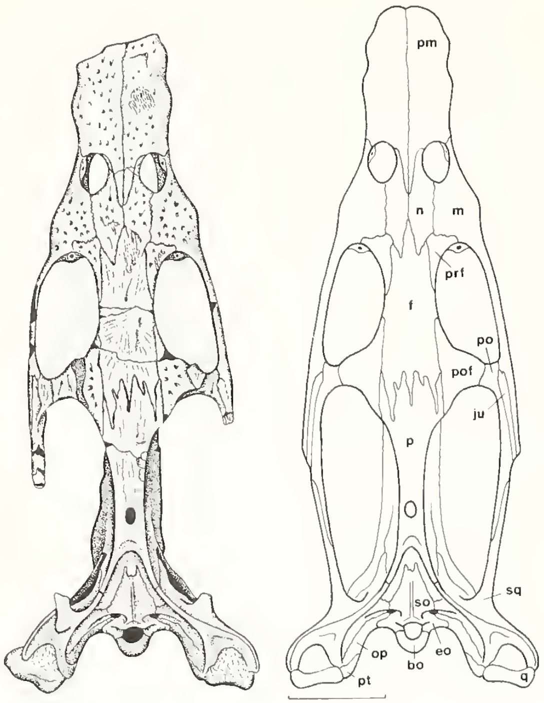
Locality and horizon. Nusslocher Zementbruch, Wiesloch near Heidelberg. Lower Trochitenkalk (mo1, Lower Hauptmuschelkalk, Anisian, Middle Triassic).

Diagnosis. A small species of *Nothosaurus* with relatively large orbits; relatively narrow postorbital arches; the pterygoids closely approach the internal nares; the paroccipital processes trend posterolaterally resulting in a distinct posterior displacement of the lower jaw joints to a level well behind the occipital condyle; the occiput is deeply concave.

Remarks. Nothosaurus juvenilis is known from a single skull only. The original condition of the skull of *Nothosaurus juvenilis* is well documented by the photographs included in Edinger's (1921*a*) thesis, and published by Haas (1963). These photographs allow the assessment of the damage suffered by the holotype as available today (Text-figs 1–3). Most importantly, the holotype suffered a break through the postorbital region, causing extensive damage to the upper temporal arches (now lost). The two parts of the skull were glued back together in an imperfect (oblique) manner (corrected for in Text-figs 3–4). The palate seems to have suffered severely, and has now been covered in its middle part by a thick layer of epoxy resin. The bone substance still preserved in this area is extremely thin, and does not allow the identification of morphological detail, nor any further preparation of the specimen.



TEXT-FIG. 1. *Nothosaurus juvenilis* Edinger. Paläontologisches und Geologisches Institut und Museum, Universität Heidelberg, König Collection, K.8698-1 (holotype); Nusslocher Zementbruch, near Heidelberg; Lower Trochitenkalk (Anisian, Middle Triassic). A, dorsal view. B, ventral view. C, lateral view. All × 1.



TEXT-FIG. 2. *Nothosaurus juvenilis* Edinger. Dorsal views of holotype; scale bar equals 20 mm. Abbreviations: bo, basioccipital; ec, ectopterygoid; eo, exoccipital; f, frontal; ju, jugal; m, maxilla; n, nasal; op, opisthotic; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; so, supraoccipital; sq, squamosal; v, vomer.

DESCRIPTION

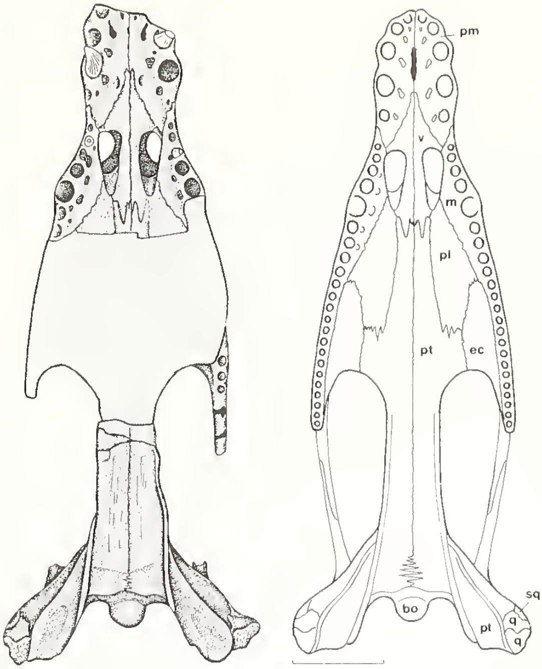
Dorsal view of the skull (Text-fig. 2). The elongated rostrum, characteristic for the genus *Nothosaurus*, is formed by the premaxillae. The premaxilla meets the maxilla at the anterolateral corner of the external naris. The posteromedial nasal process of the premaxilla enters between the external nares, extending somewhat beyond the level of their posterior margin. The premaxilla can be reconstructed to have five tooth positions, the second and fourth teeth being the largest. In between the corresponding tooth positions, the rostrum appears slightly constricted in dorsal view.

The external naris is of rounded, slightly elliptical contour. The nasal bone forms the posteromedial and, with a slender anteromedial process, the entire medial margin of the external naris. The nasal is a fairly broad, plate-like element tapering to a pointed tip posteriorly. It forms an extensive lateral contact with the maxilla, and meets the prefrontal along a well defined posterolateral contact, separating the maxilla from the anterolateral process of the frontal. The nasal bones of the two sides of the skull meet in a short suture along the dorsal midline of the skull, in between the posterior (nasal) processes of the premaxillaries and the anteromedial process of the frontal bone.

The ventral and posterolateral margin of the external naris is formed by the maxilla. In between the external naris and the orbit, the maxilla bulges laterally, indicating the position of the maxillary fangs. The maxilla defines the anterolateral and lateral margin of the orbit, the lacrimal foramen is situated entirely within the maxilla, as is characteristic for *Nothosaurus*.

The frontal bone is unpaired as a result of complete fusion of its progenitors. It enters the dorsal margin of the orbit between the prefrontal and postfrontal bones. Anteriorly, the frontal bears well defined anterolateral processes, entering between the prefrontal and the nasal bones, and an anteromedial process entering in between the paired nasals. Posteriorly, the frontal meets the parietal in a deeply interdigitating suture at the level of the postorbital arch, leaving the posterolateral processes of the frontal ill-defined.

The prefrontal bone defines the anteromedial margin of the orbit. It is well exposed in dorsal view and bears a distinct anteromedial lappet, which establishes a well defined contact with the nasal. The postfrontal bone defines the posteromedial margin of the orbit. It forms the dorsal part of a narrow postorbital arch and broadly enters the upper temporal fossa along its anteromedial margin. The postorbital bone completes the postorbital arch and defines the posterolateral margin of the orbit. Posteriorly, it extends into the (now broken) upper



TEXT-FIG. 3. *Nothosaurus juvenilis* Edinger. Ventral views of holotype; scale bar equals 20 mm. Abbreviations as in Text-fig. 2.

temporal arch. The jugal bone, situated between postorbital and maxilla, approaches the orbit rather closely but remains excluded from its posterior margin.

The parietal bone is unpaired (fused) and forms a flat and narrow parietal skull table. The pineal foramen is located at some distance from the posterior occipital crest formed by the parietal and the squamosal. The parietal gains a narrow occipital exposure, embracing the trapezoidal supraoccipital. Laterally, the parietal meets the squamosal which defines the posterior margin of the upper temporal fossa, extending anteriorly into the (now broken) upper temporal arch. The squamosal gains an occipital exposure, meeting the posterolateral corners of the supraoccipital posterior to the parietal.

Ventral view of the skull (Text-fig. 3). The palate in the holotype of *Nothosaurus juvenilis* is poorly preserved, in particular in its middle (suborbital) region. However, some important details are still discernible. The internal naris is enclosed between the vomer, maxilla, and palatine, as is characteristic for *Nothosaurus.* The vomer defines the entire anterior margin of the internal naris; the vomers enter deeply between the premaxillae with a combined anteromedial process. At the anterolateral corner of the internal naris, the vomer establishes a very narrow contact with the maxilla, apparently excluding the premaxilla from the anterolateral margin of the internal naris. However, preservation is such that a narrow entry of the premaxilla into the anterolateral margin of the internal naris cannot be entirely ruled out, although comparison with other nothosaurs supports exclusion.

The posterolateral margin of the internal naris is defined by the palatine bone which meets the vomer in the posterior margin of the choana. The posterior margin of the internal naris extends into a deep choanal groove. The pterygoid shows a bifurcated anterior tip, with its lateral prong closely approaching the posterior margin of the internal naris (choanal groove) without quite reaching it.

The morphology of the posterior part of the pterygoid is characteristic for the genus *Nothosaurus* (Rieppel 1994): deep flanges for the origin of the pterygoideus internus muscle extend all along the quadrate ramus of the pterygoid to the mandibular joint (partially broken in *Nothosaurus juvenilis*). Behind the pterygoids, the basioccipital is narrowly exposed in ventral view.

Posterior view of the skull. The occiput in the holotype of *Nothosaurus juvenilis* is not completely prepared, and the delicate condition of the skull does not allow further (acid) preparation. The detail that can be observed corresponds to the standard nothosaur morphology (Rieppel 1994). The trapezoidal supraoccipital defines the dorsal margin of the foramen magnum. The element carries a low sagittal crest. Small but well defined posttemporal fossae are located in a deep recess at the posterolateral corners of the supraoccipital. They are bordered by the supraoccipital (dorsally), squamosal (dorsolaterally), opisthotic (laterally) and exoccipital (ventrally and medially). The posterior surface of the occiput is formed by squamosal (dorsally), opisthotic and pterygoid (ventrally). The exoccipitals define the lateral margins of the foramen magnum, but they do not meet dorsal to the basioccipital. The occipital condyle, defining the ventral margin of the foramen magnum, is formed by the basioccipital only. Lateral to the occipital condyle, the basioccipital carries distinct basioccipital tubers. An eustachian foramen may open between the basioccipital tuber and the pterygoid, or the basioccipital tuber may meet the pterygoid in a closed suture (Rieppel 1994). The condition in the holotype of *Nothosaurus juvenilis* remains unclear due to incomplete preparation. Nevertheless it can be ascertained that the diameter of the basioccipital tuber is distinctly less than that of the occipital condyle.

The cranioquadrate passage is not cleared from matrix in the holotype of *Nothosaurus juvenilis*. Nevertheless, the mandibular condyle of the quadrate, defining its ventral margin, is well exposed. It is important to note that the paroccipital processes in *Nothosaurus juvenilis* trend posterolaterally to a degree which causes the displacement of the mandibular joint to a level well behind the occipital condyle.

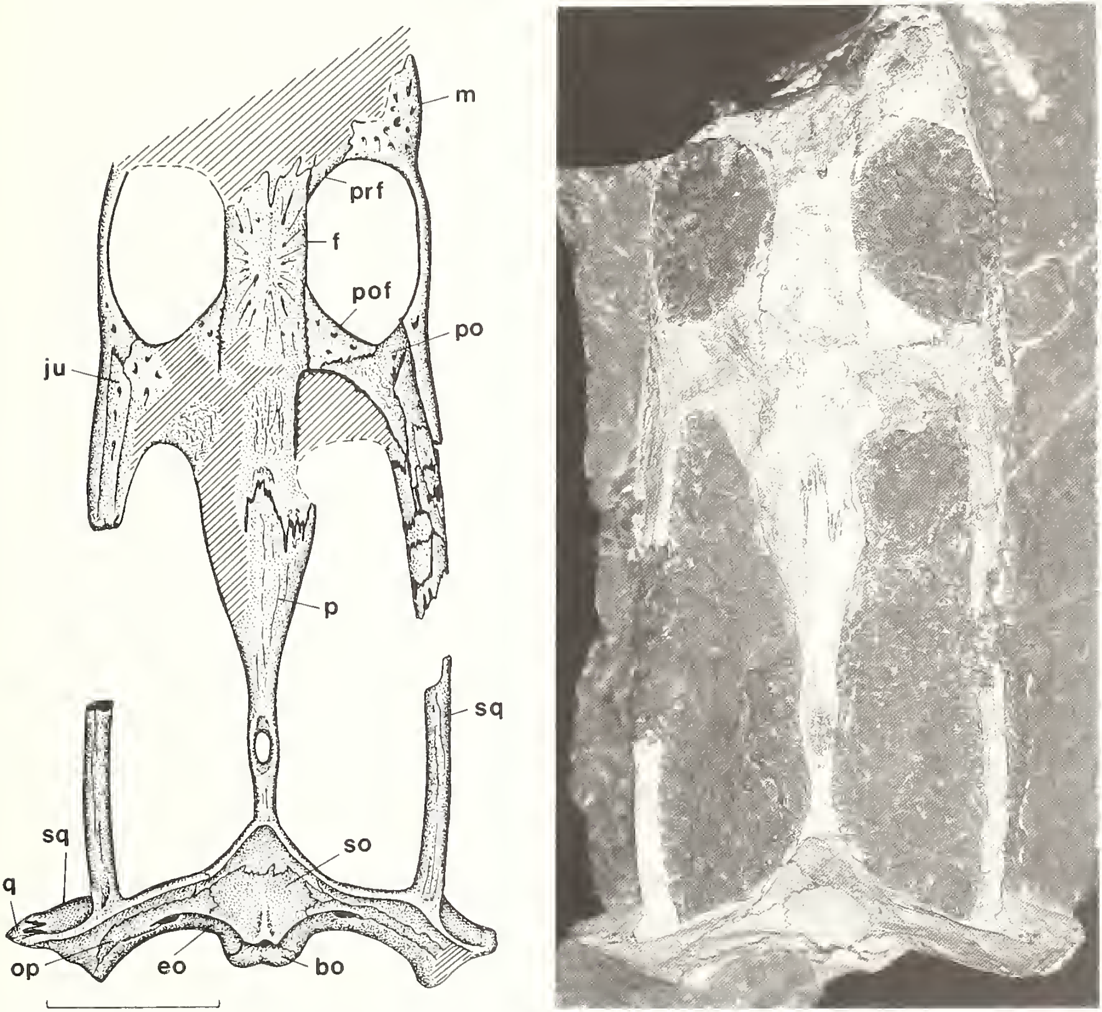
Lateral view of the skull (Text-fig. 1). Again, the lateral view of the skull would require further (acid) preparation to allow the identification of relevant detail, which is impossible due to the condition of the specimen. Nevertheless, the broad-based epipterygoid characteristic of *Nothosaurus* (Rieppel 1994) is well exposed, with deeply recessed anterior and posterior margins and a broad dorsal contact with the laterally descending flange of the parietal.

DISCUSSION

Among the described nothosaur species from the Upper Muschelkalk, *Nothosaurus juvenilis* is exceptional in its small size (apart from *N.* '*münsteri*' discussed below) and its relatively large orbits. This explains why the specimen was considered a possible juvenile of a species already known, such as *Nothosaurus mirabilis* (Edinger 1921*a*). This interpretation was disputed by Schultze (1970) on the basis of a number of morphological features characterizing *N. juvenilis* as a separate species. Indeed, the degree of ossification of the skull of *N. juvenilis* does not suggest an immature status for the specimen. The frontals have completely fused, the margins of the pineal foramen are well defined as are the sutures between braincase elements. The postfrontals enter the anteromedial margins of the upper temporal fenestrae broadly, admittedly a plesiomorphic feature but shared by no other species of *Nothosaurus* from the Upper Muschelkalk. A narrow entry of the postfrontal into the margin of the upper temporal fossa is known in some specimens from the Lower Muschelkalk (Schröder 1914), as well as in *Nothosaurus edingerae* (Schultze 1970; Rieppel and Wild 1994) from the Keuper. Derived features which distinguish *N. juvenilis* from other described species of *Nothosaurus* are, (1) the anterior extent of the pterygoid which closely approaches the posterior margin of the internal naris, in correlation with the differentiation of a deep choanal groove, and (2) the posterior displacement of the mandibular condyles of the quadrates to a level well behind the occipital condyle, resulting in a deeply excavated occiput. Other features diagnostic of *N. juvenilis* are the relatively large orbits, correlated with a relatively narrow postorbital arch. Since these characters are liable to be subject to ontogenetic variation, a close comparison of the holotype of *N. juvenilis* with other nothosaurs, particularly small specimens from the Upper Muschelkalk, seems to be in order.

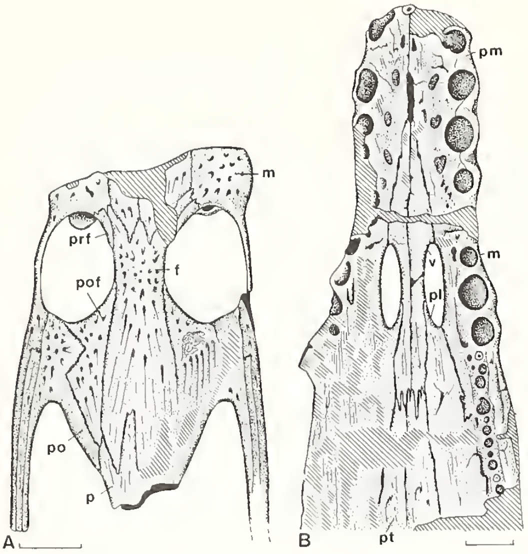
The most widespread species from the Upper Muschelkalk is *Nothosaurus mirabilis* Münster (1834; see also Meyer 1847–1855) which is of intermediate size among all nothosaurs known from the Upper Muschelkalk, but adults are distinctly larger than *N. juvenilis*. In view of the problematical status of *N. mirabilis* (diagnosed by Münster 1834 on the basis of postcranial remains and a lower jaw fragment), the specimens of that taxon primarily used for comparison in this paper are from the historical material described and figured by Meyer (1847–1855). *Nothosaurus* '*münsteri*' (Meyer, 1847–1855) is of distinctly smaller size than *N. mirabilis*, and generally considered to be represented by juvenile specimens of the latter species (Edinger 1921*a*; Schultze 1970; Kruckow 1979). However, because of its small size, the comparison of the syntypes of *N.*

'*münsteri*' (i.e. the specimens figured by Meyer 1847–1855, pl. 9) with the holotype of *N. mirabilis* is important. *Nothosaurus edingerae* is a small nothosaur from the Middle Keuper (Schultze 1970; Rieppel and Wild 1994). Finally, an as yet undescribed small nothosaur skull will be used for comparison (Text-fig. 4). It comes from the Upper Trochitenkalk (Upper Muschelkalk) of Steinsfurt, and was collected by R. H. M. König (König Collection, K-3881) who also collected the holotype of *N. juvenilis*.



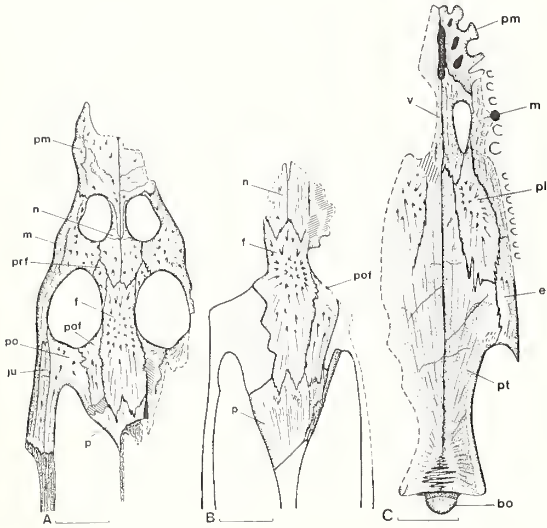
TEXT-FIG. 4. *Nothosaurus* sp. Paläontologisches und Geologisches Institut und Museum, Universität Heidelberg, König Collection, K.3881; dorsal view; drawing with abbreviations as in Text-fig. 2; Steinsfurt; Upper Trochitenkalk (Anisian, Middle Triassic); scale bar equals 20 mm.

In *N. mirabilis* (Text-fig. 5A–B), the prefrontal usually gains only a limited dorsal exposure and frequently remains separate from the nasal bone; the postfrontal is always excluded from the upper temporal fossa; interdigitation of the fronto-parietal suture may be less complex; the posterolateral lappets of the frontal bone are well defined; the vomer is relatively longer and the pterygoid widely separated from the internal nares, which show no differentiation of a choanal groove; and the



TEXT-FIG. 5. *Nothosaurus mirabilis* Münster. A, BSP 1935.I.16; anterior part of skull in dorsal view; Bayreuth; Upper Muschelkalk (Anisian, Middle Triassic). B, SMNS 56286; anterior part of palate; Berlichingen; Upper Muschelkalk (Anisian, Middle Triassic). Abbreviations as in Text-fig. 2; scale bars equal 20 mm.

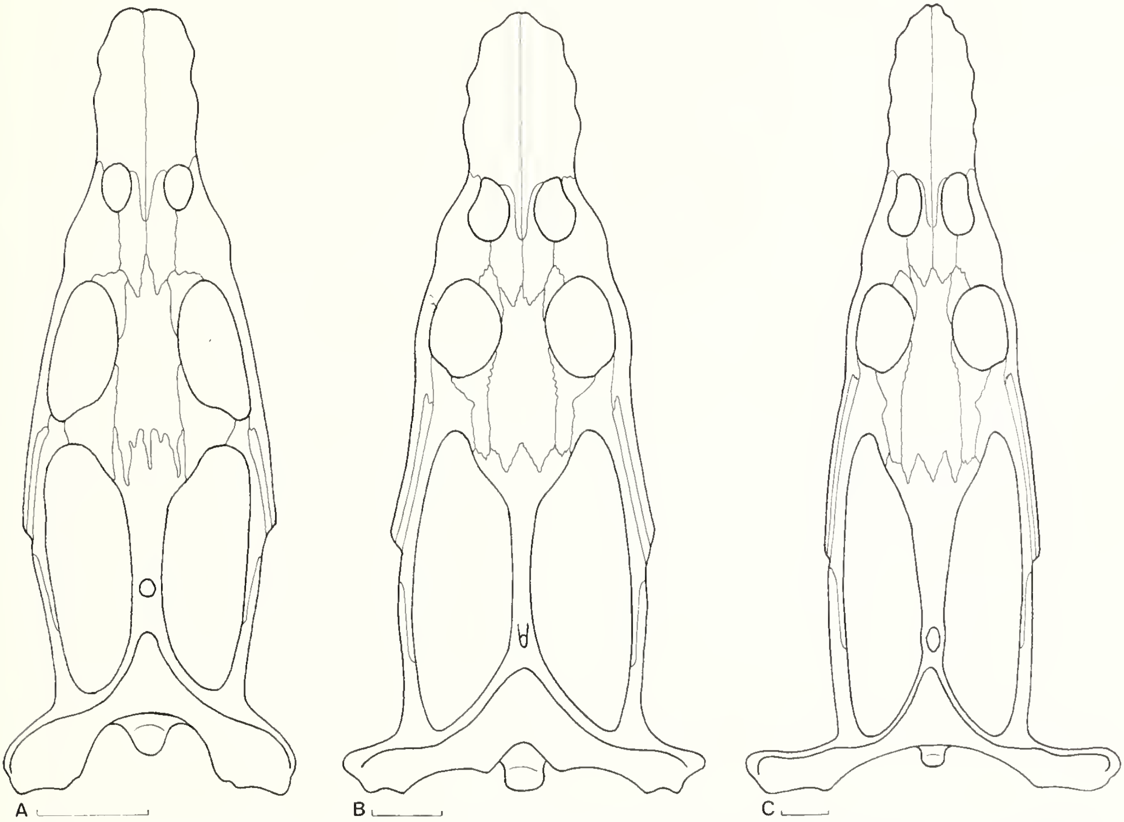
mandibular condyles of the quadrate are not displaced as far back as they are in *N. juvenilis*. *N.* '*münsteri*' closely resembles *N. mirabilis* in these features (Text-fig. 6), although one specimen (Meyer 1847–1855, pl. 9, fig. 4; see also Text-fig. 6A of this paper) shows broadly exposed prefrontals establishing a broad contact with the nasal bones, and the vomer is relatively short in another (Meyer, 1847–1855, pl. 9, fig. 2; see also Text-fig. 6C of this paper). The small *Nothosaurus* specimen from the König Collection (K-3881) also shares the same characteristics as far as preservation allows to identify them (Text-fig. 4). *N. edingerae* resembles *N. juvenilis* with respect to the narrow postorbital arch (Schultze 1970, p. 227) but otherwise differs from the latter species with respect to several characters, including a less deeply excavated occiput; the differentiation of a distinct sagittal crest formed by the parietal posterior to the pineal foramen, which lies in a deep



TEXT-FIG. 6. *Nothosaurus* '*münsteri*' (Meyer). Oberfränkisches Erdgeschichtliches Museum, Bayreuth, uncatalogued; Bayreuth; Upper Muschelkalk (Anisian, Middle Triassic). A, anterior part of skull in dorsal view; original of Meyer (1847–1855, pl. 9, fig. 4). B, skull as preserved in dorsal view; original of Meyer (1847–1855, pl. 9, fig. 6). C, skull as preserved in ventral view; original of Meyer (1847–1855, pl. 9, fig. 2). Abbreviations as in Text-fig. 2; scale bars equal 20 mm.

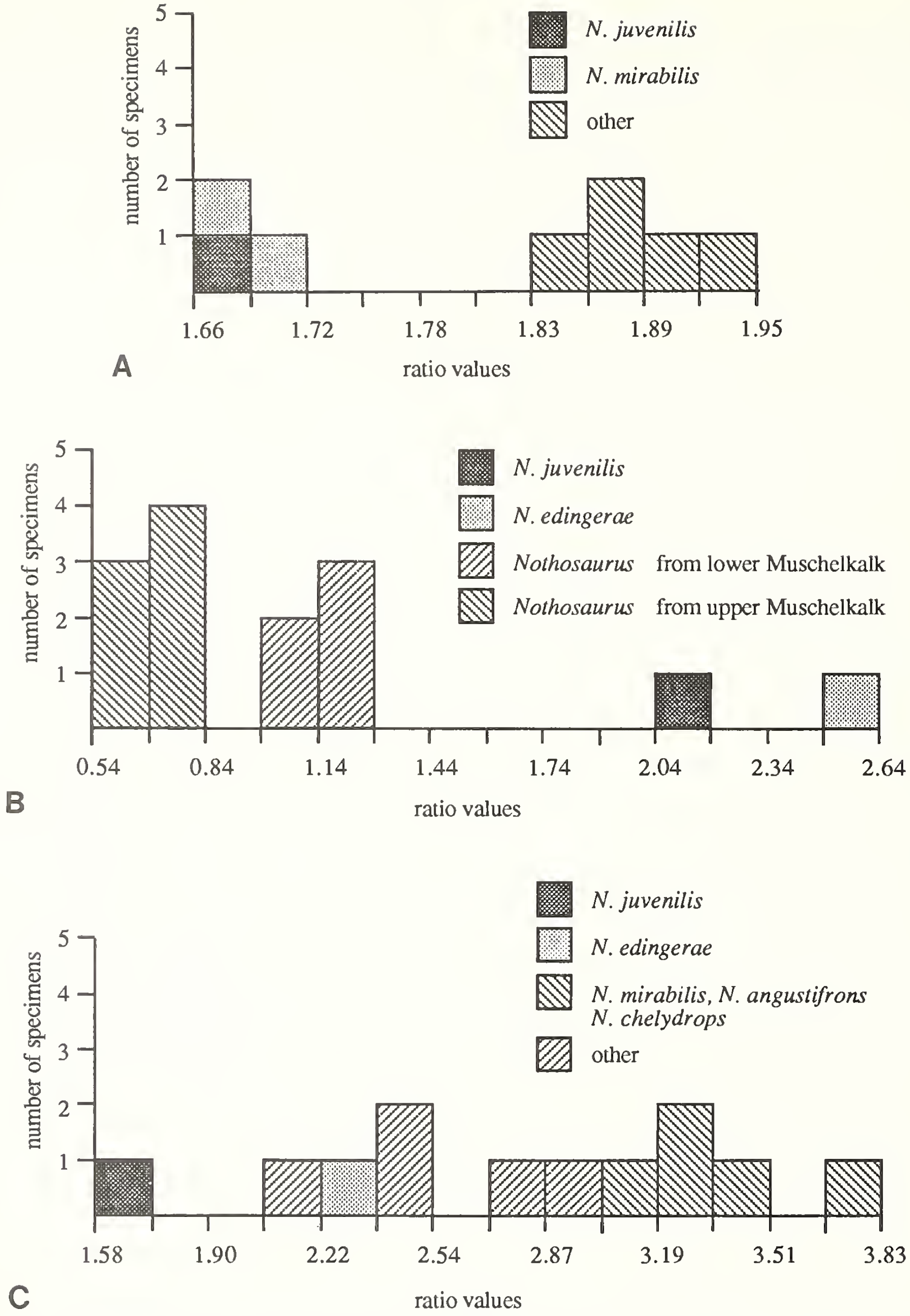
groove; and the much larger basioccipital tubers, the diameters of which exceed that of the occipital condyle (Schultze 1970; Rieppel and Wild 1994).

Proportional relations add support to the recognition of *N. juvenilis* as a separate species (Text-fig. 7), although these are often difficult to obtain because of incomplete or poor preservation of the cranial material. The rostrum in the holotype of *N. juvenilis* is broken at its anterior tip; if this damage is corrected for by the addition of 5 mm, the relative length of the rostrum falls into the range of variation of the material referred to *N. mirabilis* by Meyer (1847–1855; Text-fig. 8A). Unfortunately, the relative rostrum length remains unknown for *N.* '*münsteri*' (due to incomplete preservation). Relative rostrum length distinguishes *N. juvenilis* from the small nothosaurs of the Lower Muschelkalk described by Schröder (1914), some of which show the plesiomorphic entry of the postfrontal into the margin of the upper temporal fossa, but which all show a distinctly shorter rostrum. A relatively shorter rostrum is also characteristic of the holotype of *Nothosaurus chelydrops*, and appears to be shared by the holotype of *Nothosaurus angustifrons* (the rostrum of which is, however, incompletely preserved).



TEXT-FIG. 7. Reconstructions of nothosaur skulls in dorsal view. A, *N. juvenilis* Edinger. B, *N.* '*münsteri*' (Meyer). C, *N. mirabilis* Münster (based on Meyer, 1847–1855, pl. 2, fig. 1). Scale bars equal 20 mm.

The ratio (distance from external naris to orbit:distance from orbit to upper temporal fossa) segregates the specimens compared here into three groups (Text-fig. 8B). The first group, with values ranging from 0·55 to 0·81, comprises the historical material of *N. mirabilis* and *N.* '*münsteri*', as well



TEXT-FIG. 8. Proportional relations in the skulls of *Nothosaurus* listed in Appendix 2. A, ratio (distance from tip of snout to anterior margin external naris: distance from tip of snout to anterior margin external orbit). B, ratio (distance from external naris to orbit: distance from orbit to upper temporal fossa). C, ratio (longitudinal diameter upper temporal fossa: longitudinal diameter orbit). For further discussion see text.

as the holotypes of *N. angustifrons* Meyer and *N. chelydrops* Fraas. The second group, with values ranging from 1·03 to 1·27, comprises the small nothosaurs from the Lower Muschelkalk described by Schröder (1914). (It should be noted that inclusion of other, as yet undescribed, *Nothosaurus* skulls from the Upper Muschelkalk causes a narrow overlap in that ratio between *N.* cf. *mirabilis* and the Lower Muschelkalk species – personal observation). The value of 2·1 reflects the narrow postorbital arch in *N. juvenilis*, approached only by *N. edingerae* with a value of 2·5–2·7 (Schultze 1970).

The narrow postorbital arch of *N. juvenilis* may be a consequence of its large orbits, as is the low value (1·58) of the ratio (longitudinal diameter upper temporal fossa: longitudinal diameter orbit). All other specimens compared here show continuous variation between values of 2·13 to 3·43 (Text-fig. 8C). It is interesting to note that the small specimens or species of *Nothosaurus* from the Lower Muschelkalk described by Schröder (1914), *N.* '*münsteri*', *N. edingerae* and the *Nothosaurus* sp. from the König Collection (K-3381) fall into the lower range of these values (2·13–2·98) while *N. mirabilis*, *N. angustifrons* and *N. chelydrops* range from 2·72–3·43, thus indicating a negative allometric growth of the orbit. However, even the small species of *Nothosaurus* from both the Lower and Upper Muschelkalk, and *N. edingerae* from the Keuper, some very close to *N. juvenilis* in absolute size, show relatively smaller orbits and (with the exception of *N. edingerae*) a relatively broader postorbital arch. This indicates that ontogenetic variation alone is not a sufficient explanation for the relative size of the orbits in *N. juvenilis*.

CONCLUSION

The recognition of *Nothosaurus juvenilis* as a separate taxon on the basis of morphological characteristics as well as skull proportions indicates the presence of a small species of *Nothosaurus* in the Upper Muschelkalk, different from the medium-sized species *Nothosaurus mirabilis* and a large species of as yet problematic synonymy (*Nothosaurus* '*andriani*' Meyer, *N.* '*baruthicus*' Geissler, *N.* '*giganteus*' Münster, '*Paranothosaurus*' Peyer; cf. Schultze 1970, for a discussion). A similar pattern of taxic diversity is observed in the Lower Muschelkalk, with the small species of *Nothosaurus* described by Schröder (1914) coexisting with a large species known from as yet undescribed, very incomplete material (personal observation). Likewise in the Keuper, the small *Nothosaurus edingerae* (Upper Keuper) may have overlapped in geographical and temporal distribution with the large *Nothosaurus chelydrops* (Lower Keuper), if some incompleteness of the fossil record is assumed. A better diagnosis of all the terminal taxa within the genus *Nothosaurus* is still required, as is a well supported cladogram indicating their phylogenetic interrelationships. However, the general pattern which only just begins to emerge from the revision of the genus *Nothosaurus* is one of niche-partitioning, the coexisting species segregating into different size classes with presumably different trophic preferences.

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APPENDIX I

Measurements of *Nothosaurus juvenilis* (König Collection, K.8698-1). The tip of the rostrum is incomplete (broken); 5 mm have been added to rostrum length for the computation of the proportional relations discussed in the text and Text-figure 8. Measurements given below refer to the rostrum as preserved on the right side of the skull. All measurements are given in mm; values in parentheses are for the left side of the skull.

Tip of the snout to posterior margin of the mandibular condyle of quadrate:	137·2
Tip of the snout to occipital condyle:	126·2
Tip of the snout to posterior margin of supraoccipital:	121·0
Tip of the snout to posterior margin of occipital crest of parietal:	105·1
Tip of the snout to anterior margin of upper temporal fossa:	74·0 (75·0)
Tip of the snout to anterior margin of the orbit:	44·5 (47·2)
Tip of the snout to anterior margin of the external naris:	24·5 (26·4)
Tip of the snout to the anterior margin of internal nares:	27·5 (27·1)
Longitudinal diameter of external naris:	8·7 (8·5)
Transverse diameter of external naris:	6·4 (6·2)
Longitudinal diameter of orbit:	26·5 (25·9)
Transverse diameter of orbit:	16·0 (14·4)
Longitudinal diameter of upper temporal fossa:	42·0 (41·0)

Longitudinal diameter of internal naris:	12·5 (13·0)
Transverse diameter of internal naris:	4·2 (41·0)
Distance from posterior margin of external naris to anterior margin of orbit:	11·5 (12·0)
Distance from posterior margin of orbit to anterior margin of upper temporal fossa:	5·7 (5·5)
Mid-dorsal bridge between external nares:	6·0
Mid-dorsal bridge between orbits (minimal width)	11·2
Mid-dorsal bridge between upper temporal fossae (behind the pineal foramen):	6·5
Longitudinal diameter of pineal foramen:	4·3
Transverse diameter of pineal foramen:	2·7
Distance from pineal foramen to posterior edge of parietal:	6·3
Vertical diameter of foramen magnum:	6·5
Horizontal diameter of foramen magnum:	8·5

APPENDIX 2

Comparative material included in this study and used in the computation of Text-figure 8. Institutional abbreviations are as follows: Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich – BSP; Museum für Naturkunde, Humboldt Universität, Berlin – MB.R.; Oberfränkisches Erdgeschichtliches Museum, Bayreuth – BT; Senckenberg Museum, Frankfurt a.M. – SMF; Staatliches Museum für Naturkunde, Stuttgart – SMNS.

Nothosaurus angustifrons Meyer: SMNS 51972 (holotype).

Nothosaurus chelydrops Fraas: SMNS 7162 (holotype).

Nothosaurus edingerae Schultze: SMF R-4035 (holotype); referred material: SMNS 59072.

Nothosaurus marchicus Koken: MB.R. 2 (counterpart of holotype).

Nothosaurus mirabilis Münster: BT uncatalogued: original to Meyer (1847–1855, pl. 2, fig. 1–2; pl. 3, fig. 1); original to Meyer (1847–1855, pl. 3, fig. 2; pl. 34, fig. 1); original to Meyer (1847–1855, pl. 6, figs 1–3; pl. 7, fig. 1); BT uncatalogued, undescribed; BSP 1935.I.16.

Nothosaurus '*münsteri*' (Meyer): BT uncatalogued: original to Meyer (1847–1855, pl. 9, figs 1–3); original to Meyer (1847–1855, pl. 9, fig. 4); original to Meyer (1847–1855, pl. 9, figs 6–7).

Nothosaurus oldenburgi Schroeder: MB.R. 1 (holotype).

Nothosaurus procerus Schroeder: MB.R. 4 (holotype).

Nothosaurus procerus var. *parva*: MB.R. 5 (holotype).

Nothosaurus raabi Schroeder: MB.I. 007.18 (holotype).

Nothosaurus cf. *raabi*: MB.R. 24 (undescribed specimen).

Nothosaurus sp.: Geologisch–Paläontologisches Institut, Ruprecht-Karls-Universität, Heidelberg, König Collection, K-3881.

THE TAXONOMIC STATUS OF THE UPPER LIASSIC ICHTHYOSAUR *EURHINOSAURUS LONGIROSTRIS*

by C. McGOWAN

ABSTRACT. The swordfish-like ichthyosaur *Eurhinosaurus*, primarily from the German Upper Liassic, is generally considered to be monotypic. The authority of the type species, *E. longirostris*, has usually been given as Jaeger, 1856, but it is shown that Mantell, 1851 is the correct authority. The subject of Mantell's description (BMNH 14566) is from the Upper Liassic of Yorkshire. Recent preparation confirms the presence of an abbreviated mandible, confirming its eurhinosaurian status. *E. longirostris* (Mantell 1851) is thus unequivocally the type species of *Eurhinosaurus*, and BMNH 14566 is the holotype. *Eurhinosaurus huenei* Swinton, 1930, is shown to be a junior synonym of *E. longirostris*.

THE Upper Liassic (Toarcian) ichthyosaur *Eurhinosaurus* is unusual in having a mandible which is only about half the length of the skull. Like its living analogue, the swordfish (*Xiphias*), *Eurhinosaurus* is a monotypic genus (Huene 1931; McGowan 1979) and the type species is generally considered to be *E. longirostris*. However, there has been considerable confusion in the literature regarding the use of the specific name, the appropriate authority, and whether the original material was a eurhinosaur at all. Owen (1881, p. 124), for example, cited himself as author of the name, and included specimens from the lower and upper divisions of the English Liassic, one of which is probably referrable to *Leptopterygius tenuirostris* (BMNH 36182, McGowan 1989). Most other sources (e.g. Huene 1922; Kuhn 1934) have cited Jaeger 1856 as the author, but this too is incorrect (McGowan 1974). The resolution of the problem hinges on a single specimen and the condition of its mandible, for which new information is now available. The purpose of the present paper is fourfold: to review the history of the specific name *E. longirostris*; to assess the status of the critical specimen; to discuss the monotypic status of the genus *Eurhinosaurus*; and to give a synonymy for the valid species.

MATERIALS AND METHODS

The institutional abbreviations used are: BMNH, the Natural History Museum, formerly called the British Museum (Natural History), London, UK; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Measurements in excess of 550 mm were made with a steel tape and recorded to the nearest millimetre. Large vernier callipers and small dial callipers were used for smaller measurements, recorded to the nearest 1 mm and 0·1 mm respectively. The measurements referred to in the text are defined in Table 1.

TAXONOMIC HISTORY OF *E. LONGIROSTRIS*

The name *Ichthyosaurus longirostris* was first published by Mantell (1851, p. 385) in a guide to the palaeontological galleries of the old British Museum, where one of the ichthyosaurian specimens on display was described as follows: 'ICHTHYOSAURUS LONGIROSTRIS – Wall-case E. – In the middle compartment of Case E there is part of the skeleton of an Ichthyosaurus from Whitby, about six feet in length. It is remarkable for the exceedingly slender and elongated muzzle; the skull is

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TABLE 1. Characters recorded and ratios derived.

Character or ratio	Description
Vertebral count to pelvis	Number of vertebrae from atlas to level of pelvis
Vertebral count to tailbend	Number of vertebrae from atlas to level of tailbend
Skull length	Distance between tip of snout and posterior edge of quadrate
Snout length	Distance between tip of snout and anterior (internal) margin of orbit
Orbital diameter	Internal diameter of orbit measured along its longitudinal axis
Forefin length	Distance between distal end of humerus and most distal phalanx, measured between horizontals perpendicular to longitudinal axis of forefin
Forefin width	Maximum width measured between verticals, parallel to longitudinal axis of forefin
Forefin aspect ratio	Forefin length divided by forefin width

crushed; and with the exception of the chain of vertebrae which extends to the tail, and a few bones of one paddle, there are no characteristic parts preserved. The specific name, longirostris, is affixed to this specimen; but I cannot ascertain that it is figured or described.'

According to Article 12 of the ICZN (1985, third edition), names published before 1931 must have been accompanied by a description of the taxon. The above narrative, as noted elsewhere (McGowan 1974, p. 25), is sufficiently detailed to recognize the specimen, and therefore constitutes a description. Thus Lydekker (1889, p. 91), identified it as BMNH 14566, noting that it was figured by Owen (1881, pl. 32, fig. 8). *I. longirostris* therefore became available in 1851, with Mantell as the author and BMNH 14566 as the holotype.

BMNH 14566 is from the Upper Liassic of Whitby, Yorkshire, England, and comprises a dorsoventrally compressed skull, most of the vertebral column, and a partial forefin. The skull is remarkable for the extreme length and slenderness of the snout, as noted by Mantell, and is far more tenuous than in the common English long-snouted species, *Leptopterygius tenuirostris*. Since the skull was exposed from the dorsal aspect, Mantell would not have been able to determine whether the mandible was abbreviated. He would have had no reason to suspect that it might have been because no such ichthyosaur had ever been found.

Jaeger (1856) described three specimens from the Upper Liassic of Germany that he believed to belong to the same species as the Whitby specimen described by Mantell (1851). One of Jaeger's specimens clearly depicted a shortened mandible (1856, pl. 30, fig. 2), and he made the obvious comparison with the swordfish *Xiphias*. Jaeger referred his material to *I. longirostris*, but gave the authority as Owen and Jaeger rather than Mantell. This may have been because Mantell had not demonstrated the shortened mandible; Jaeger's reason for sharing the credit of authority with Owen was probably because of the correspondence he had with Owen prior to publishing the paper.

The genus *Eurhinosaurus* Abel, 1909 was erected, almost parenthetically, in a paper describing the Miocene cetacean *Eurhinodelphis cocheteuxi*. Abel noted that it was not certain whether the cetacean's mandible extended to the tip of the snout, or whether it was abbreviated as in the ichthyosaur which had been classified as *Ichthyosaurus longirostris*. He considered that the attenuated mandible of *I. longirostris*, together with numerous other distinguishing features, warranted erecting a separate genus, for which he proposed the name *Eurhinosaurus*. The type species, by monotypy, is *Eurhinosaurus longirostris* (Mantell).

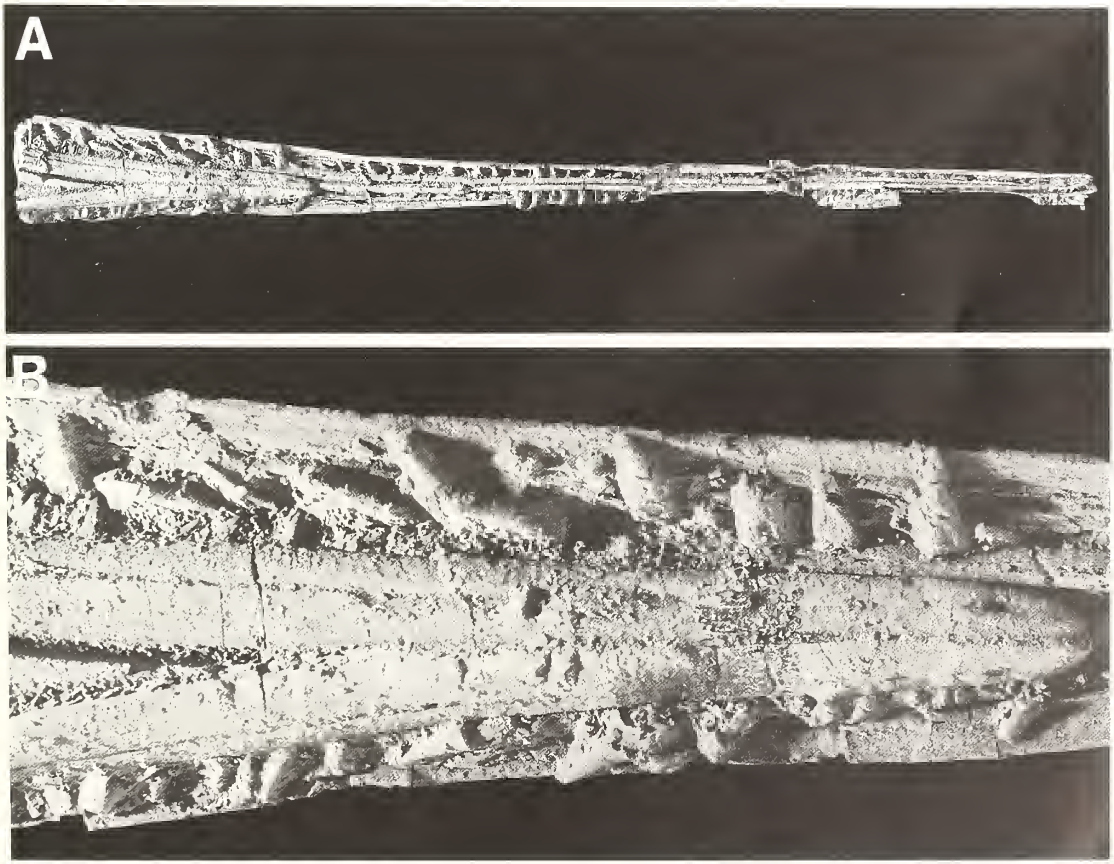
Huene (1922) referred Mantell's specimen (BMNH 14566) to the predominantly German species *E. longirostris*, but without giving any detailed reasons. Although the skull is dorsoventrally compressed, it is possible to obtain some approximate measurements. The skull and snout are

TABLE 2. Comparison of the skulls of BMNH 14566 and R5465. All measurements in millimetres.

Specimen	Locality	Skull length	Snout length	Orbital diameter
BMNH 14566	Whitby	≈ 860	≈ 680	≈ 100
BMNH R5465	Holzmaden	1035	870	125

approximately 860 mm and 680 mm long respectively, and the diameter of the orbit is approximately 100 mm. The snout measurement is not inconsistent with that of a specimen of *L. tenuirostris* of this size, but the orbit is relatively too small, comparable instead with that of *Eurhinosaurus*. When compared with a eurhinosaur skull (BMNH R5465) of similar size, the measurements were found to be proportionally similar (Table 2). From this evidence it was tentatively concluded that BMNH 14566 probably was referable to *Eurhinosaurus* (McGowan 1989), but confirmation was required.

Preparation now demonstrates that the specimen does have an abbreviated mandible, and it is therefore unquestionably referable to *Eurhinosaurus* (Text-fig. 1). This is fortunate for nomenclatural



TEXT-FIG. 1. *Eurhinosaurus longirostris* (Mantell). Holotype, BMNH 14566. A, the rostral portion, from about the level of the external nares to the tip of the snout, separated from the rest of the skull and shown from the ventral aspect; ×0·24. B, closeup to show the abbreviated mandible; ×1·0.

stability because it establishes the propriety of the name *Eurhinosaurus longirostris* (Mantell), with BMNH 14566 as the holotype.

The holotype comprises a partial vertebral column, part of a forefin, and a skull that is exposed from the dorsal aspect. Most of the bone appears to be embedded in original matrix, and the whole has been set in a plaster surround, encased in a wooden frame. The skull is about 860 mm long and has a long slender snout. Most of the rostral section of the skull, from a natural break just anterior of the external naris to its tip, was removed from the plaster prior to preparation. Removal of the adhering matrix and plaster revealed a much abbreviated mandibular section that is about 172 mm long (Text-fig. 1).

THE STATUS OF *EURHINOSAURUS HUENEI*

Huene (1928) described a new and complete skeleton of *Eurhinosaurus* that had just been purchased by the British Museum (Natural History) from Hauff's workshop in Holzmaden. At that time, only two other skeletons of *Eurhinosaurus* were known, one of which (SMNS 14931) was complete and quite well preserved. Huene noted that the new specimen (BMNH R5465), which was smaller than the other two, differed in the following regards.

1. In BMNH R5465, there were forty five presacral vertebrae and forty seven vertebrae between the sacrum and tailbend, compared with forty eight and forty in SMNS 14931. Thus the vertebral count to the tailbend in the BMNH R5465 and SMNS 14931 was ninety two and eighty eight respectively.
2. The coracoid of BMNH R5465 had a narrower (anterior) notch than in SMNS 14931.
3. The forefin was slender with three notched elements, whereas the fin was usually wider and without notching.
4. The ischium and pubis were wider medially than in some other specimens.
5. The hindfin had numerous notched elements, whereas there were only two or three in the other two specimens.

Huene concluded that BMNH R5465 probably represented a new species, but postponed formalizing this until more material became available. Drevermann (1930) reported that a complete skeleton of a large individual had been acquired by the Senckenberg Museum in Frankfurt (SMF 4155). Swinton (1930), impressed by the differences that Huene (1928) had enumerated, and by the fact that BMNH R5465 differed from SMF 4155 too, erected the new species, *E. huenei* with BMNH R5465 as the holotype. Huene's (1928) description was considered sufficiently detailed that a redescription was unnecessary, and Swinton's diagnosis was largely based on the features that Huene had described. Like Huene (1928), Swinton (1930) discussed the immaturity of BMNH R5465, but he did not think that the differences could be attributed to immaturity, nor did he consider sexual dimorphism to be a factor, although Huene (1928) had suggested that this may have been true for some of the features.

Huene (1931) described SMF 4155, together with several other specimens of *Eurhinosaurus*. He disagreed with Swinton's erection of a second species, believing that *Eurhinosaurus* was a monotypic genus comprising one markedly variable species. He held the same opinion twenty years later, after several additional specimens had been found (Huene 1951), and discussed the possibility that some of the variation may have been attributed to sexual dimorphism. I find this a persuasive argument because there is some evidence of a dichotomy in certain features that are not size-related and which cannot be attributed to growth (McGowan 1979).

The significance of the differences between BMNH R5465 and the other specimens can be considered by examining each of the five features enumerated above.

1. Swinton (1930) and Huene (1928) were in close agreement with the number of presacral vertebrae in BMNH R5465, namely 44 and 45 respectively, but I counted 50, which is close to the mean value of 48, the observed range for the species being 45–50 ($n = 7$). BMNH R5465 is therefore not atypical, but the observed range is wider than it is in other taxa. In *Stenopterygius quadriscissus*, for example, it is 42–45 ($n = 13$), while in *Leptopterygius tenuirostris* and *Ichthyosaurus communis*,

the observed ranges are 45–47 ($n = 6$) and 42–44 ($n = 9$) respectively. The count of 92 vertebrae to the tailbend is not atypical, the observed range being 91–95 and the mean being 92 ($n = 7$).

2. Notwithstanding the fact that notching in the coracoid tends to be variable and is therefore not a useful diagnostic character, Huene (1931) pointed out that the notch in BMNH R5465 was similar to that of SMF 4155.

3. The occurrence of notching in the fins, like the fin proportions themselves, is usually variable. For example, in *S. quadriscissus* the number of notched elements in the forefin varies between two and six (McGowan 1979). The forefin of BMNH R5465 has three notched elements, whereas this varies between zero and one in the other specimens. Given the variability in this feature, this discrepancy is not considered significant. A measure of the relative slenderness of the forefin is given by the aspect ratio. BMNH R5465 is said to be more slender than the other specimens, and this is reflected in the high value of 4·03 for the aspect ratio. However, this falls within the observed range for the other material (2·68–4·09, $n = 6$). The extreme variability of this character is reflected in the discrepancy in values between left and right fins within the same individual. For example, in SMF 4155 the aspect ratio is 3·75 in one forefin and 2·94 in the other.

4. The ischium of BMNH R5465 is much wider medially (i.e. ventrally) than in the other specimens, but there is some variation in the proportions of the pelvic elements among the specimens. It is also possible that the ischium is abnormal because the pelvis is unusual for having a fused pubis and ischium on the right side, whereas the elements are unfused on the left side. The pubis is not wider than in the other material and, aside from the asymmetrical fusion with the ischium, it is unremarkable.

5. The hindfin has fourteen notched elements on the right side and sixteen on the left, compared with between two and five among the other specimens. This is a much wider discrepancy than in the forefin, and is the only significant difference among these five features.

Thus BMNH R5465, the holotype of *E. huenei*, differs from the other referred specimens only in having more notched elements in the hindfin. Given the variability in the occurrence of notching in ichthyosaurian fins, this is not considered sufficient grounds for the erection of a new species and *E. huenei* is considered to be a junior synonym of *Eurhinosaurus longirostris*.

SYSTEMATIC PALAEONTOLOGY

The taxonomy at the family level is in need of revision and, as this lies beyond the scope of the present work, no familial designation will be given here. For each reference in the synonymy the name is as attributed (wrongly) by that author.

Class REPTILIA
Order ICHTHYOSAURIA Blainville, 1835
Genus EURHINOSAURUS Abel, 1909

Locality and horizon Upper Liassic (Toarcian) of Whitby, Yorkshire, England, and of Holzmaden and surrounding areas of southern Germany.

Type species. E. longirostris.

Eurhinosaurus longirostris (Mantell)

1851	*Ichthyosaurus longirostris* Mantell, p. 385.
1856	*Ichthyosaurus longirostris* Owen and Jaeger; Jaeger, p. 948, pl. 30.
1881	*Ichthyosaurus longirostris* Owen [*partim*]; Owen, p. 124, pl. 32, fig. 8.
1889	*Ichthyosaurus latifrons* König [*partim*]; Lydekker, pp. 89, 91.
1891	*Ichthyosaurus longirostris* Jaeger; Fraas, p. 63, pl. 11, figs 2, 4; pl. 12, fig. 5; pl. 14, fig. 10.
1909	*Eurhinosaurus longirostris*; Abel, p. 245.

1922 *Ichthyosaurus longirostris* Jaeger; Huene, p. 32, pl. 5; pl. 9, figs 3–4; pl. 12, fig. 1.
1928 *Eurhinosaurus* sp.; Huene, pl. 37.
1930 *Eurhinosaurus huenei* Swinton; Swinton, p. 275.
1931 *Eurhinosaurus longirostris*; Huene, p. 30, pl. 3, fig. 1.
1951 *Eurhinosaurus longirostris* Jaeger; Huene, p. 277, fig. 1; pl. 18.
1989 *Eurhinosaurus huenei* Swinton; McGowan, p. 116, figs 7–8; pl. 5, figs 2, 4.

Holotype. BMNH R5465.

Type locality and horizon. Whitby, Yorkshire, England. Upper Liassic (Toarcian); more precise stratigraphical data are wanting (see Lydekker 1889, p. 91).

Referred material. Specimens as listed by McGowan (1979, p. 116).

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THE EARLY CRETACEOUS PTERODACTYLOID PTEROSAUR *COLOBORHYNCHUS* FROM NORTH AMERICA

by YUONG-NAM LEE

ABSTRACT. *Coloborhynchus wadleighi*, a new pterosaur from the Paw Paw Formation (upper Albian), Texas, is closely related to an English species *Coloborhynchus clavirostris*. A dentulous partial snout shows unique tooth arrangement and a dorsal medial crest on the anterior portion of the premaxilla. This is the first tooth-bearing pterodactyloid pterosaur known from North America. The genus *Coloborhynchus* is assigned to the family Ornithocheiridae.

CRETACEOUS pterodactyloid pterosaurs previously recognized in North America are referred to the families Nyctosauridae, Pteranodontidae, and Azhdarchidae (*sensu* Wellnhofer 1991*a*). The Nyctosauridae and Pteranodontidae are best known in North America from the Niobrara Formation (Coniacian to Campanian) of western Kansas (Marsh 1872, 1876; Miller 1972). The Azhdarchidae are from the Judith River Formation (Campanian) in Alberta, Canada (Currie and Russell 1982), the Two Medicine Formation (Campanian) of Montana (Padian and Smith 1992), and the Javelina Formation (Maastrichtian) of Big Bend National Park, Texas (Lawson 1975).

In the Lower Cretaceous of North America, pterodactyloid pterosaurs are represented by three humeri. *Bennettazhia oregonensis* (Gilmore) is from the Hudspeth Formation (Albian), Oregon (Gilmore 1928; Nessov 1991), and an indeterminate pteranodontid humerus is known from the Mowry Shale of Montana (*sensu* Bennett 1989). The third humerus is an azhdarchid from the Glen Rose Formation (uppermost Aptian to lower Albian), Texas (Murry *et al.* 1991).

A new pterosaur specimen was discovered in the Paw Paw Formation (upper Albian), Fort Worth, Texas. It is a partial snout preserved in three dimensions. The snout has teeth and a pronounced sagittal crest. The presence of teeth clearly distinguishes the new specimen from toothless forms of North American pterodactyloid pterosaurs previously recognized from cranial remains.

OCCURRENCE

The specimen (SMU 73058, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas) was discovered in 1992 in the Paw Paw Formation, Tarrant County, Texas (Text-fig. 1). The Paw Paw Formation was named by Hill (1894) for exposures of an 18 m thick ferruginous sand and clay sequence found along Paw Paw Creek in northeast Denton and Grayson counties, Texas. Southward from the type locality, it thins and typically comprises more marine facies (Perkins and Albritton 1955). In the Tarrant County area, the formation is a brown to yellow, fossiliferous clay (8 m thick), with scattered sandstone partings. The age of the Paw Paw is between 100 and 97·5 Ma in this area, based on invertebrate faunas (Jacobs *et al.* 1994). Its environment of deposition has been interpreted to be predominantly nearshore marine, including deltaic and estuarine environments (Scott *et al.* 1978).

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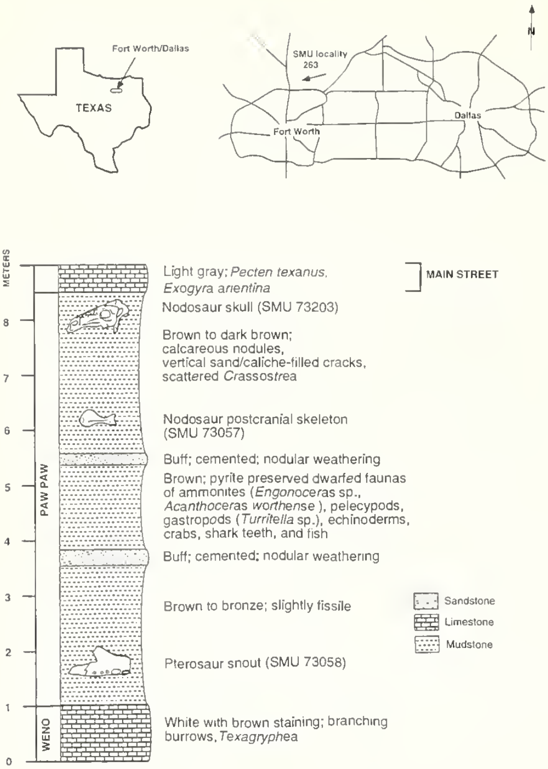
Fort Worth/Dallas
TEXAS
SMU locality 263
N
Dallas
Fort Worth
METERS
8
7
6
5
4
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PAW PAW
WENO
Light gray; *Pecten texanus*, *Exogyra arientina*
MAIN STREET
Nodosaur skull (SMU 73203)
Brown to dark brown; calcareous nodules, vertical sand/caliche-filled cracks, scattered *Crassostrea*
Nodosaur postcranial skeleton (SMU 73057)
Buff; cemented; nodular weathering
Brown; pyrite preserved dwarfed faunas of ammonites (*Engonoceras* sp., *Acanthoceras worthense*), pelecypods, gastropods (*Turritella* sp.), echinoderms, crabs, shark teeth, and fish
Buff; cemented; nodular weathering
Brown to bronze; slightly fissile
Pterosaur snout (SMU 73058)
White with brown staining; branching burrows, *Texagryphea*
Sandstone
Limestone
Mudstone

TEXT-FIG. 1. SMU locality 263 in Tarrant County, Texas, and stratigraphical section of the Paw Paw Formation. Inset shows major highways in Dallas/Forth Worth.

SYSTEMATIC PALAEONTOLOGY

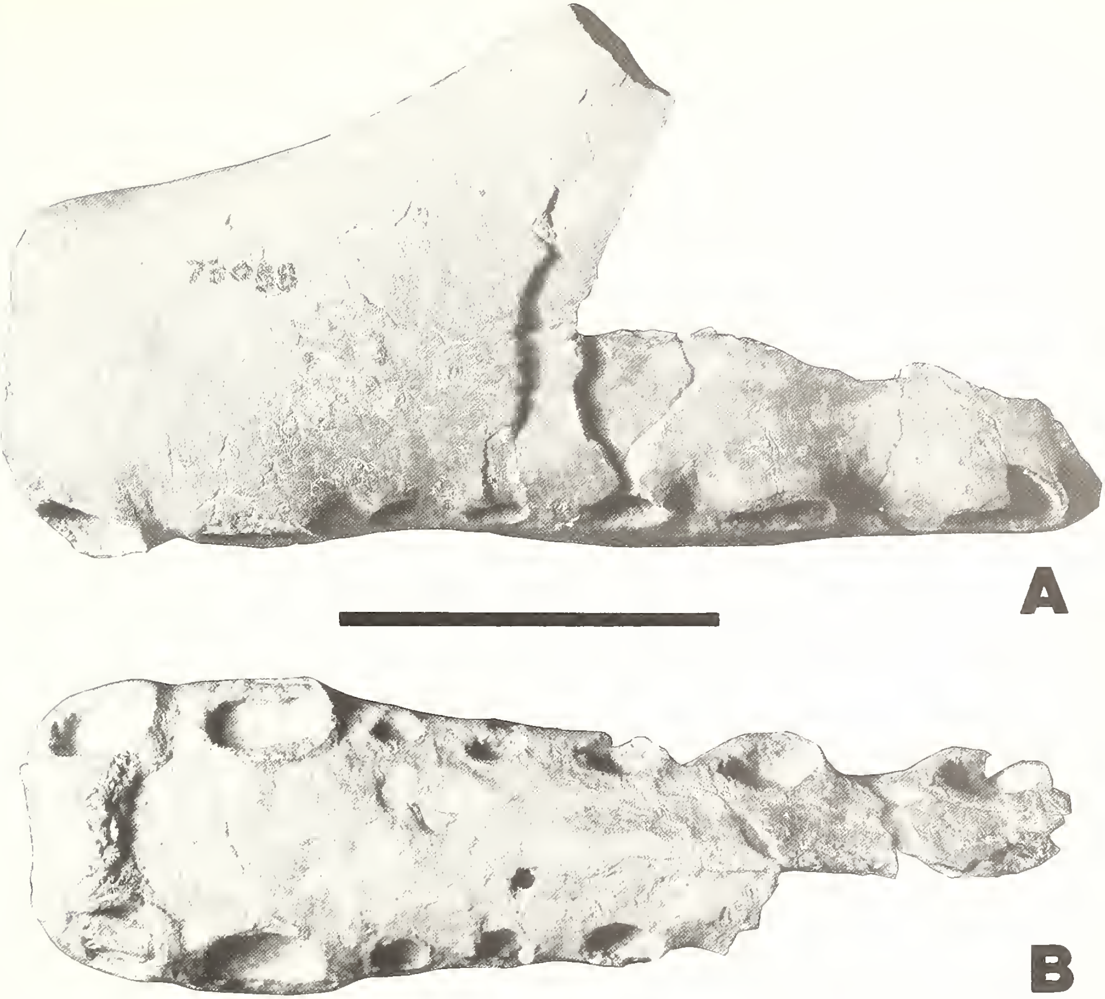
Order PTEROSAURIA Kaup, 1834
Suborder PTERODACTYLOIDEA Plieninger, 1901
Family ORNITHOCHEIRIDAE Seeley, 1870
Genus COLOBORHYNCHUS Owen, 1874

Type species. *Coloborhynchus clavirostris* Owen, 1874.

Age and distribution. Berriasian to Valanginian of the Hastings Sands, St. Leonard's-on-Sea, UK, and Albian of the Paw Paw Formation, Fort Worth, Texas, USA.

Diagnosis. (Modified after Owen 1874.) The flattened anterior margin of the premaxilla is triangular in shape. A pair of teeth project anteriorly from the blunt anterior margin at a significant elevation above the palate relative to subsequent teeth. A median depression occurs on the anterior margin. The medial crest rises from near the tip of the snout.

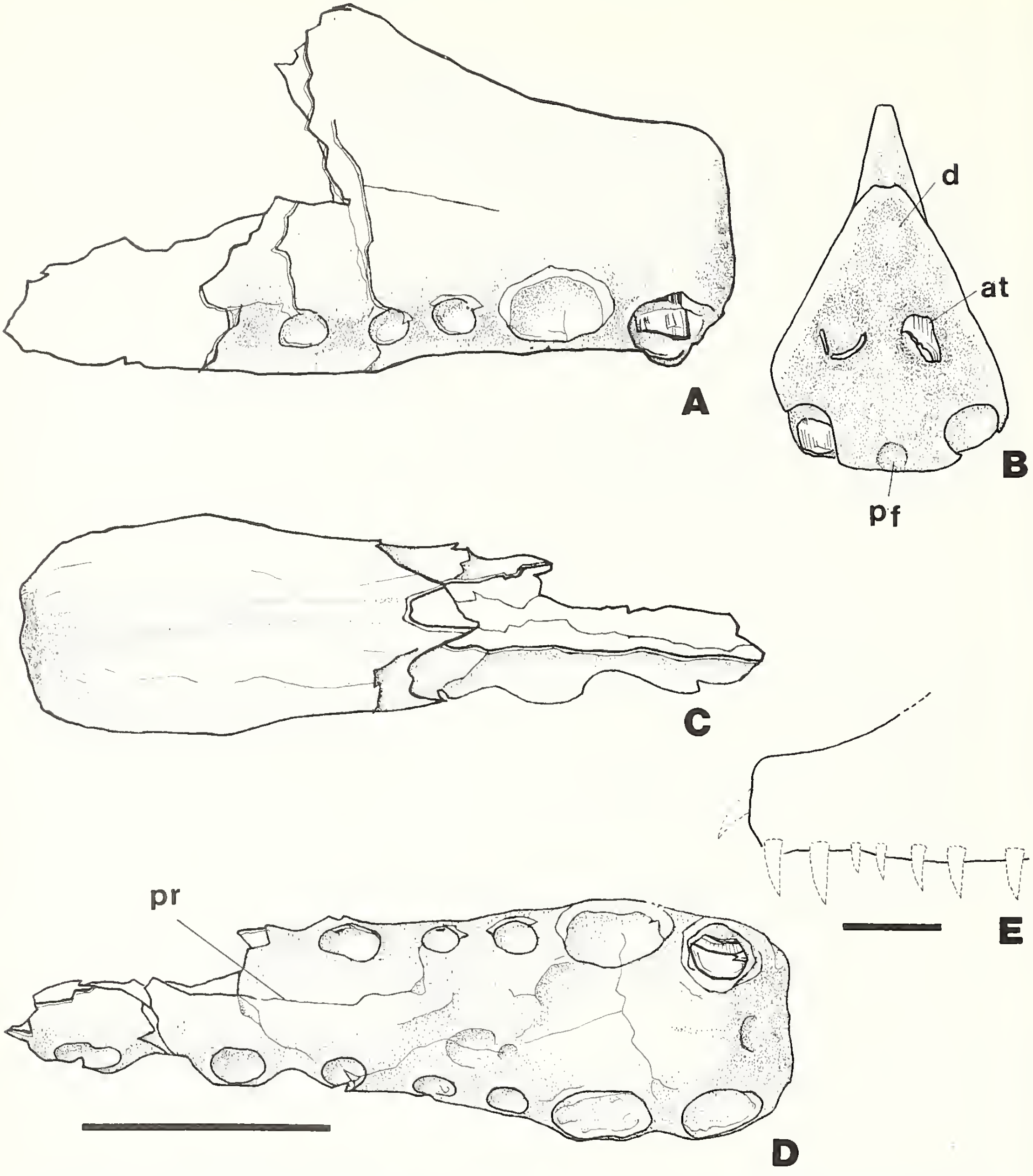
Discussion. The taxonomic history of *Coloborhynchus* is complex. Seeley (1869) grouped numerous fragments of jaws and odd bones of pterosaurs from the Cambridge Greensand into two genera, *Ptenodactylus* and *Ornithocheirus*. His original diagnosis for the genus *Ornithocheirus* was 'no teeth anterior to the palate' (Seeley 1869, p. 16). It included three species, and had for its type *Pterodactylus sinus* of Owen. In 1870, Seeley's book *The Ornithosauria* was published, in which he abandoned the genus *Ptenodactylus* and referred all of the species described from the Cambridge Greensand to *Ornithocheirus*, incorrectly interpreting the type of *Pterodactylus sinus* to be a lower jaw. He rediagnosed the genus *Ornithocheirus* as 'having teeth prolonged anterior to the muzzle,' and as 'having a palate with a longitudinal ridge' (Seeley 1870, p. 112). However, Owen (1874) did



TEXT-FIG. 2. *Coloborhynchus wadleighi* sp. nov.; SMU 73058, holotype; Tarrant County, Texas; Paw Paw Formation (Albian); partial snout in left lateral (A) and palatal (B) views. Scale bar represents 50 mm.

not consider *Ornithocheirus* to be valid and did not accept Seeley's conclusion that *Pterodactylus simus* belonged to *Ornithocheirus* because it is not a lower jaw. He stated 'I have no evidence, and Mr Seeley has given none, of such departure from the Pterosaurian type of hand as would justify the term *Ornithocheirus* proposed by Mr Seeley for *Pterodactylus sedgwickii* in his 'Ornithosauria' in 1870' (Owen 1874, p. 6). This circumstance led Owen to establish the new generic names, *Coloborhynchus* and *Criorhynchus*, abandoning *Ornithocheirus* in 1874.

Coloborhynchus was named for pterosaurs that have 'the foremost pair of teeth projecting forward in the upper jaw from the truncate surface at a higher level than the alveolar border' (Owen 1874, p. 6). Describing the type species, *Coloborhynchus clavirostris*, a partial snout from the Hastings Sands of the Wealden, Owen (1874) referred two other species to this genus, *Coloborhynchus cuvieri* and *C. sedgwickii*. The former was originally named by Bowerbank as *Pterodactylus cuvieri* for the anterior part of the upper jaw from the Lower Chalk of Kent at the meeting of the Zoological Society, January 14th, 1851, and the latter was described as *Pterodactylus sedgwickii* for the anterior parts of a skull and mandible from the Upper Greensand of Cambridge



TEXT-FIG. 3. *Coloborhynchus wadleighi* sp. nov.; SMU 73058, holotype; Tarrant County, Texas; Paw Paw Formation (Albian). A–D, partial snout in right lateral (A), anterior (B), dorsal (C) and palatal (D) views. E, reconstructed dentition in left lateral view. Abbreviations: at, anterior tooth; d, depression; pf, pneumatic foramen; pr, palatal ridge. Scale bars represent 50 mm.

(Owen 1859). They had been renamed *Ornithocheirus cuvieri* and *O. sedgwickii* according to Seeley's (1870) definition of *Ornithocheirus* prior to their referral to *Coloborhynchus*.

Coloborhynchus clavirostris has a medial crest. Owen (1874) described this character as 'the flattened fore part of premaxillary is broader and of less height in *Coloborhynchus clavirostris* before the narrow upper surface begins to slope backward to the contour of the cranium' (Owen 1874, p. 7; pl. 1, figs 1–4). However, he did not include this character in the definition of *Coloborhynchus*. Owen believed *Ornithocheirus* (*sensu* Seeley 1870) was invalid and therefore included *Ornithocheirus cuvieri* and *O. sedgwickii* in his new genus *Coloborhynchus* because they shared anteriorly projecting teeth. Neither has a medial crest. To distinguish a blunt-snouted specimen with no anteriorly projecting teeth from *Coloborhynchus*, he also renamed *Pterodactylus simus*, described by himself in 1861, as *Criorhynchus simus*.

In 1881, Seeley naturally regarded *Coloborhynchus* as a synonym of *Ornithocheirus*. Citing *Coloborhynchus cuvieri* and *C. sedgwickii* as examples, he mentioned *Coloborhynchus* as follows: 'I am unable to detect any difference between Prof. Owen's definition of that genus and my previous definition in 1870 of *Ornithocheirus*' (Seeley 1881, p. 16). Therefore, *Coloborhynchus clavirostris*, which has different characters from *C. cuvieri* or *C. sedgwickii*, was implied to belong to *Ornithocheirus* (Seeley 1881).

The systematic position of *Ornithocheirus* became more and more obscure because various incomplete pterosaur bones have been referred to this genus. Hooley (1914) tried to divide the cranial material from the Cambridge Greensand, referred to the genus *Ornithocheirus* by Seeley (1870), into five named groups. Owen's two referred species of *Coloborhynchus* (*C. cuvieri* and *C. sedgwickii*) were referred to Hooley's Group 1 with the generic name *Ornithocheirus*. He knew that *Coloborhynchus clavirostris* could be distinguished from *Ornithocheirus* by its medial crest and put it into his Group 4, *Criorhynchus*. He also made it clear that *Criorhynchus simus*, the type of *Ornithocheirus*, is an upper, not a lower jaw, by the presence of a longitudinal ridge on the palate.

Owen (1874) had some doubts about the validity of *Criorhynchus*. He considered that this genus may represent a specimen of *Coloborhynchus* with shed and unreplaced anterior teeth. However, Hooley (1914) believed that *Coloborhynchus clavirostris* was a synonym of *Criorhynchus simus* in which erosion had worn the tip of the snout to expose the bases of the teeth. Thus, *Coloborhynchus* disappeared with the synonymy of *C. clavirostris* with *Criorhynchus simus*. Wellnhofer (1978, 1987) accepted the synonymy of *Coloborhynchus clavirostris* and *Criorhynchus simus*, and placed the species in the separate family Criorhynchidae.

The new material reported here clearly validates Owen's view that the two genera are distinct. The anterior margin of *Coloborhynchus clavirostris* is duplicated in the Texas specimen and is not water-worn. *Coloborhynchus clavirostris* is not a synonym of *Criorhynchus simus*. Therefore, the species should be resurrected and the genus *Coloborhynchus* is also valid with modification.

Coloborhynchus wadleighi sp. nov.

Text-figures 2–3

Holotype. SMU 73058, Shuler Museum of Paleontology, Southern Methodist University; a partial snout.

Type locality and horizon. Paw Paw Formation (Lower Cretaceous, upper Albian), Tarrant County, Texas, USA (SMU locality 263, exact location on file at SMU).

Diagnosis. Snout with flattened anterior margin from which projects a pair of anteroventrally directed teeth. An oval median depression lies above the anterior teeth. A pneumatic foramen occurs between the second pair of teeth. The second and third pairs of teeth are large and project vertically as shown by the orientation of the tooth sockets. The medial crest has a concave anterior margin beginning at the tip of the snout and rising posteriorly.

Derivation of name. *wadleighi*, in honour of Mr Chris Wadleigh, who found the specimen.

Description. The specimen is a partial snout with a median crest formed at least in part by the premaxillae (Text-fig. 2). Posterior parts of the skull including the nasopreorbital opening are missing. The cortical bone is thin (0·5–0·8 mm) and dark yellowish brown. Delicate buttresses and struts are developed on the internal surface of the bone. This architecture, along with the thin cortical bone, persuasively shows the lightness of pterosaurian construction for flight. The crest extends from the tip of the snout and is concave as far as preserved. The concave margin of the flange as preserved represents the arc of a circle with a diameter of 240 mm, limited by a chord of 75 mm. The crest decreases in width continuously from the lateral margins of the jaw dorsally to where it forms a thin ridge (Text-fig. 3C). The ridge is approximately 4 mm wide at its narrowest. The midline forms a shallow gutter.

The rugose, flattened anterior margin of *C. wadleighi* is shaped like an acute triangle in anterior view. The corners of the triangle are rounded (Text-fig. 3B). A small pneumatic foramen lies between the second pair of teeth. The alveoli for a pair of anterior teeth are in the middle of the anterior margin, and at a greater elevation above the tooth sockets of the second pair of teeth. The anterior teeth projected anteroventrally. Just above the anterior teeth there is a shallow oval depression. The second pair of teeth occurs at the corners of the base of the anterior triangle. They project ventrally.

In palatal view (Text-figs 2B, 3D), the snout is expanded anteriorly. A broad ridge on the palate projects below the level of the tooth sockets and runs posteriorly from the fourth pair of tooth sockets. Eight oval alveoli are preserved on the left side, six on the right in this specimen. All tooth sockets on the palate face ventrally and their long axes are arranged anteroposteriorly. The tooth arrangement is somewhat peculiar (Text-fig. 3E). The middle three tooth pairs (4th, 5th, and 6th from the anterior) of *C. wadleighi* are approximately half the size of the more anterior and posterior teeth. The third tooth is the largest and the fourth tooth the smallest in this specimen, as estimated from the sizes of the alveoli (Table 1). The base of the second right tooth, oval in cross section, is preserved. The maximum diameter of this tooth is 9·2 mm.

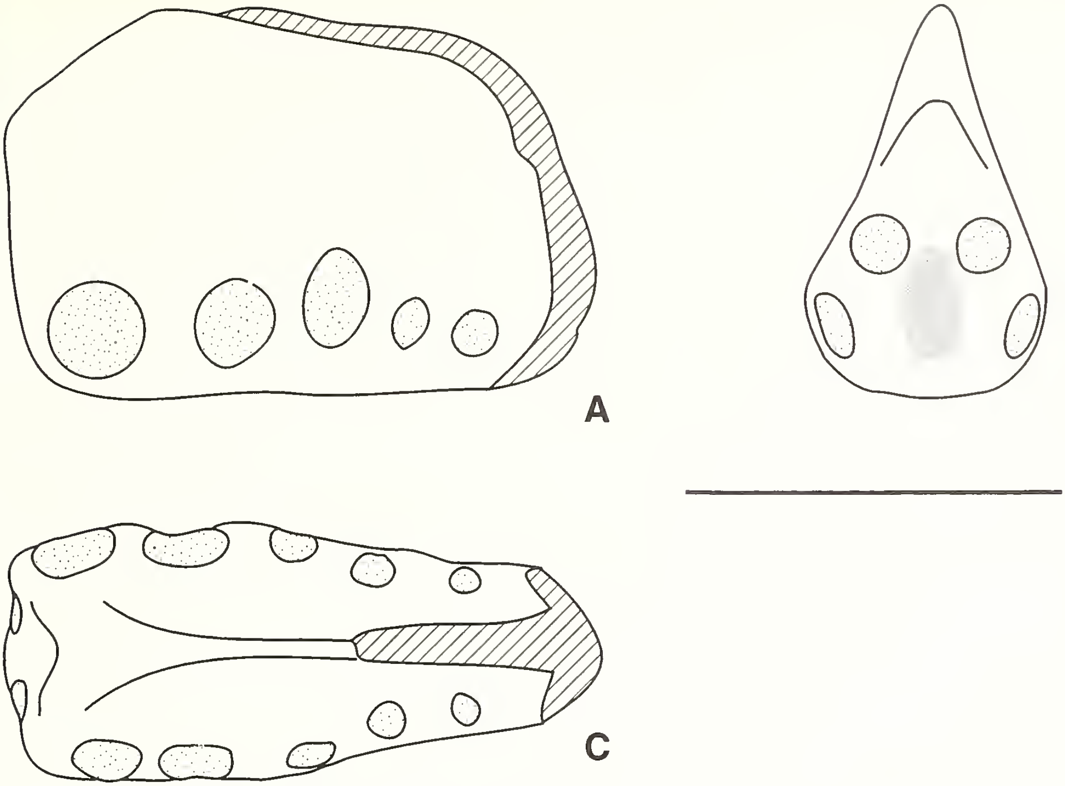
TABLE 1. Measurements in mm of maximal diameters of alveoli (anterior = 1).

	1st	2nd	3rd	4th	5th	6th	7th	8th
Left	13·0	15·0	17·7	7·2	7·9	9·8	13·6	14·3
Right	13·0	13·8	17·6	7·3	7·4	9·7	–	–

Comparisons. Coloborhynchus wadleighi can be compared to *C. clavirostris* (Text-fig. 4) in the position of the anterior oval depression, the crest angle, and the size and position of teeth based on sockets. An oval median depression is developed above the anterior teeth in *C. wadleighi*, while it is below the anterior teeth in *C. clavirostris*. The crest angle of *C. wadleighi* begins lower than that of *C. clavirostris* (approximately 15° and 45°, respectively). Both snouts are expanded anteriorly, but the position of tooth sockets is different in each. The palate of *C. wadleighi* is flat and teeth project ventrally. In *C. clavirostris*, the anterior three tooth sockets are ventrolaterally displaced relative to the row of subsequent teeth. The anterior three pairs of teeth are sub-equal and project ventrolaterally (Unwin 1991). In *C. wadleighi*, the first two pairs of palatal teeth are larger than the succeeding teeth.

Coloborhynchus cuvieri and *C. sedgwickii*, which Owen (1874) referred along with the type species, are excluded from *Coloborhynchus* by the absence of a median depression on the anterior margin and a medial crest rising from the snout. They are referred to *Ornithocheirus* (Seeley 1881; Hooley 1914; Wellnhofer 1978).

Discussion. Coloborhynchus can be distinguished easily from other dentulous crested-snout pterosaurs, *Anhanguera*, *Criorhynchus*, and *Tropeognathus*. *Anhanguera* is one of the best known pterosaurs from the Santana Formation (Aptian), Araripe Plateau, Brazil. The type species (*A. blittersdorffi*) was described and a separate family, the Anhangueridae, was erected for it by Campos and Kellner (1985). One of its conspicuous features is the 'presence of an enlargement of the distal (anterior) part of the skull, where the premaxillar (*sic*) teeth, the biggest teeth of all, are found' (Campos and Kellner 1985, p. 459). Wellnhofer (1991*c*) rediagnosed *Anhanguera*, the most remarkable character being the low medial crest anterior to the nasopreorbital opening, but not extending to the tip of the snout. The most distinct difference between *Coloborhynchus* and



TEXT-FIG. 4. *Coloborhynchus clavirostris* Owen; holotype; Wealden Hastings Sands; partial snout in left lateral (A), anterior (B), and palatal (C) views (drawn from Owen 1874); shadow area in B shows oval depression; scale bar represents 50 mm.

Anhanguera is the position of the medial crest. While the crest of *Anhanguera* does not extend to the tip of the snout, in *Coloborhynchus* it begins at the anterior margin of snout. Unlike *Coloborhynchus*, the crest of *Anhanguera* is thin (Campos and Kellner 1985, pl. 2, text-fig. 1), even at the base, which often causes it to be broken off. In contrast, the crest of *Coloborhynchus* decreases in width continuously from the lateral margins of the jaw to the dorsal edge where it forms a thin ridge (Text-fig. 3C). The anterior end of the snout of *Anhanguera* is not blunt but acute. The first and second teeth of *A. santanae* (AMNH 22555, American Museum of Natural History, New York) project anteroventrally (Wellnhofer 1991*b*, text-fig. 2), while in *Coloborhynchus* the second tooth projects ventrally from palate.

Wellnhofer (1987) assigned *Tropeognathus* from the Santana Formation to the Criorhynchidae (Hooley 1914, Group 4). The family was originally erected on the basis of fragmentary skull material of *Criorhynchus simus* from the Cambridge Greensand, England (Owen 1861). Affinity of the two genera is supported by similar high medial crests at the front end of the skull and the dentition. The laterally compressed anterior snouts without teeth of criorhynchids are clearly distinct from *Coloborhynchus*, which has a blunt triangular anterior end from which prominent anterior teeth project. In addition, the crest of *Coloborhynchus* is concave from the tip of the snout, in contrast to the convex and steep crest of *Criorhynchus* and *Tropeognathus*.

The Ornithocheiridae are based on *Ornithocheirus* (Seeley 1870, = subfamily Ornithocheirae), and are defined by two characters: ‘teeth are prolonged anterior to the muzzle, and the palate has a longitudinal ridge’. The snout of *Coloborhynchus* exhibits these characters. Therefore, it is assigned to the family Ornithocheiridae.

The similarity between the Brazilian and the English Early Cretaceous pterosaurs has been suggested using as examples *Tropeognathus* and *Criorhynchus*, or *Araripesaurus* and *Ornithocheirus* (Wellnhofer 1987; Unwin 1988). However, the relationships of North American pterosaurs with English and South American pterosaurs have always been a puzzle. This is due to the very patchy fossil record of Early Cretaceous pterosaurs in North America. Therefore, the discovery of *Coloborhynchus wadleighi* is important because it is the first record that shows affinity with English pterosaurs in the Early Cretaceous. Although the phylogenetic relationships between *Coloborhynchus wadleighi* and other North American pterodactyloid pterosaurs are uncertain, it lived in North America prior to the flourishing of edentulous forms in the Late Cretaceous.

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AN EOCENE PECCARY FROM THAILAND AND THE BIOGEOGRAPHICAL ORIGINS OF THE ARTIODACTYL FAMILY TAYASSUIDAE

by STÉPHANE DUCROCQ

ABSTRACT. Recent field work in the upper Eocene Krabi Basin (south Thailand) has yielded several dental and postcranial remains of a new genus and species, *Egatochoerus jaegeri*, of a tayassuid morphologically very close to the upper Eocene North American genus *Perchoerus*. According to the somewhat more primitive morphology of the Thai species, the family Tayassuidae seems to have originated in South East Asia, and then migrated into the New World as early as late Eocene. The familial status of the alleged tayassuid *Odoichoerus uniconus* from the lower Oligocene of China is also reconsidered, and this species should be referred to the Suidae on the basis of its dental and mandibular morphology.

PECCARIES are pig-like ungulates belonging to the family Tayassuidae (including the genera *Tayassu* and *Dicotyles*) and are now confined to North and South America, where they occupy an ecological niche resembling that of the Suidae. Peccaries differ from the pigs mainly in their somewhat smaller size, their downwardly directed upper canines (in suids, they curve more or less outward and upward), in their fused third and fourth metatarsals, and in having four toes on the front feed and three on the hind feed (Nowak and Paradiso 1984).

Unambiguous Tayassuidae appeared in Europe during the early Oligocene with the genus *Propalaeochoerus* Stehlin, 1899 (Hellmund 1992), and during the middle Oligocene with *Doliochoerus quercyi* Filhol, 1882 (Ginsburg 1974). The family appeared in North America in the late Eocene (middle Chadronian; see Stucky 1992) with the genera *Perchoerus* Leidy, 1869 (up to the middle Oligocene = Whitneyan) and *Tinohyus* Marsh, 1875 (sometimes considered as a synonym of *Perchoerus*) in the early Oligocene (Orellan).

Only a few tayassuids are known from the Palaeogene of Asia. The most ancient possible representatives of this group come from the upper Eocene of northern China (a new genus cited from the Naduo Formation, *in* Russell and Zhai 1987). An indeterminate tayassuid has also been reported from southern China (Gongkang Formation, Bose and Yongle basins) at the Eocene-Oligocene boundary by Xu (1982), and then attributed to a new genus, '*Eopecarihyus*', but never published. Finally, the species *Odoichoerus uniconus* Tong and Zhao, 1986 was created for a fragmentary lower jaw, probably from the same locality (Tong and Zhao, 1986).

The Tayassuidae diversified considerably over the entire northern hemisphere (in North America from the late Eocene to Recent, in Asia from the late Eocene to the late Miocene, and in Europe from the early Oligocene to the late Miocene), and in a large part of the southern hemisphere (in Africa from the early Oligocene to the early Pliocene and in South America from the lower Pliocene to Recent).

Dental and postcranial remains have been collected from the upper Eocene localities of Wai Lek and Bang Pu Dam (Krabi Basin, see Ducrocq *et al.* 1992) in Thailand (which also yielded numerous remains of anthracotheres, see further), and are attributed to a new genus and species of Tayassuidae. These elements do not display significant size and structural differences from one locality to another, and are assumed to represent a single species.

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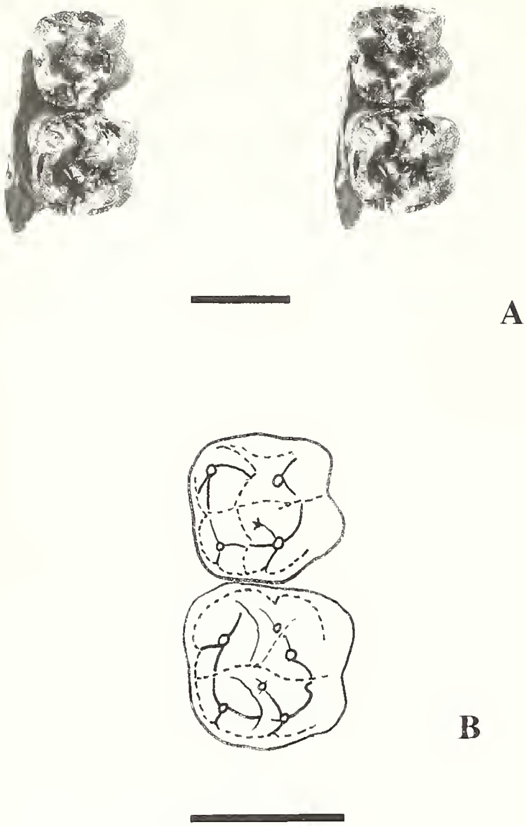


TEXT-FIG. 1. *Egatochoerus jaegeri* gen. et sp. nov. Bang Pu Dam, Thailand; upper Eocene. A, TF 2672; right maxilla with M1/-M2/, occlusal view, stereo pair; scale bar = 10 mm. B, interpretative drawing of the same specimen. Scale bar = 10 mm.

SYSTEMATIC PALAEONTOLOGY

Order ARTIODACTYLA Owen, 1848
Family TAYASSUIDAE Palmer, 1897
Genus EGATOCHOERUS gen. nov.

Type species. Egatochoerus jaegeri sp. nov.

Derivation of name. From EGAT (Electricity Generating Authority of Thailand), the company which mines the lignite in Krabi and which has allowed us to work in the lignite mines for several years.

Diagnosis. As for species.

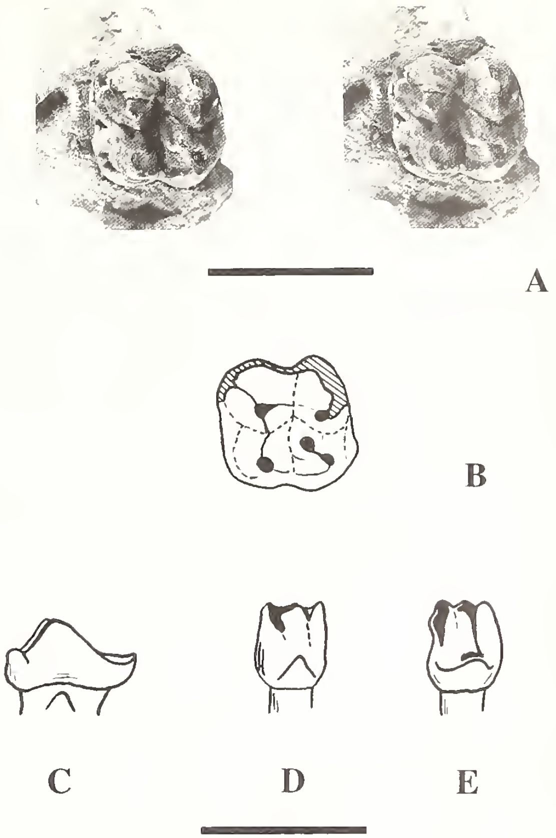
Egatochoerus jaegeri sp. nov.

Derivation of name. In honour of Professor J.-J. Jaeger, the discoverer of the holotype.

Holotype. A right lower jaw with C and P/2-M/3; Specimen No. TF 2681, Collections of the Department of Mineral Resources, Bangkok.

Type locality. Lignite mine, Bang Pu Dam, Krabi Basin, southern Thailand (latitude, about 8° N; longitude, about 99°E).

Horizon. Thin lignite seam 10 metres below the base of the main lignite seam (Formation B2, see Bristow 1991); Krabi Tertiary Basin, upper Eocene (see Ducrocq *et al.* 1991, 1992 for discussion about the age).



TEXT-FIG. 2. *Egatochoerus jaegeri* gen. et sp. nov. Bang Pu Dam, Thailand; upper Eocene. A, TF 2826; right upper DP4/, occlusal view, stereo pair. B, interpretative drawing of the same specimen; scale bar = 10 mm. TF 2681. C–E, interpretative drawings of right lower P/4; C, lingual view; D, mesial view; E, distal view. Scale bar = 10 mm.

Other material. Fragmentary left lower jaw with P/3-M/3 (TF 2825, Bang Pu Dam), fragmentary right maxillary with P4/-M1/ (TF 2674, Wai Lek), fragmentary right maxillary with M1/-M2/ (TF 2672, Wai Lek), fragmentary left maxillary with DP4/(TF 2826, Wai Lek), left M2/ (TF 2827, Wai Lek), right M1(?)/(TF 2673, Bang Pu Dam), isolated left I/2 (TF 2967, Bang Pu Dam), isolated right I/3 (TF 2968, Bang Pu Dam), isolated right I1/ (TF 2969, Bang Pu Dam), right astragalus (TF 2813, Bang Pu Dam) associated with a right calcaneum (TF 2814, Bang Pu Dam), right astragalus (TF 2812, Bang Pu Dam).

Diagnosis. Tayassuid close to *Perchoerus* in its dental morphology. Size similar to that of *Odoichoerus uniconus*. Mandible deep, becoming shallower anteriorly, with a well developed angular process, and unfused symphysis. Vertical lower canine with triangular cross-section, premolars increasing in size distally, diastema between C and P/2, P/1 lost, P/4 with two main cusps (protoconid and metaconid), lower molars with a deep waist between the two lobes and M/3 with strong hypoconulid. Upper molars with four main cusps and two (mesial and distal) lingually situated accessory cusps, fused internal roots, system of grooves ('Furchenplan' of von Hünermann) poorly expressed. Astragalus morphologically close to that of *Tayassu*.

Distinguished from *Perchoerus* by loss of P/1, an M/3 with more massive hypoconulid, a more simple P4/ and by upper molars with less developed accessory cusps and weaker cingula. Differs from *Doliochoerus* in its smaller size, more rectilinear and more massive lower canine, deeper mandible, lower premolars with a greater size differential from front to rear and in having upper molars with weaker crests. *Egatochoerus* is smaller than *Palaeochoerus* and it further differs from it by having a more massive mandible and by its upper molars with weaker crests, stronger accessory cusps and no lingual cingula. *Egatochoerus* differs from *Propalaeochoerus* in its deeper lower jaw, squared molars and more simple P/4.

Description. The upper cheek teeth display an easily recognizable structure. On TF 2674, P4/ displays a lingual conical cusp (protocone) with a mesial crest well developed and directed towards the labial cusp, which is lacking on this specimen. A slightly crenulated cingulum occurs mesially and distally as a tiny shelf.

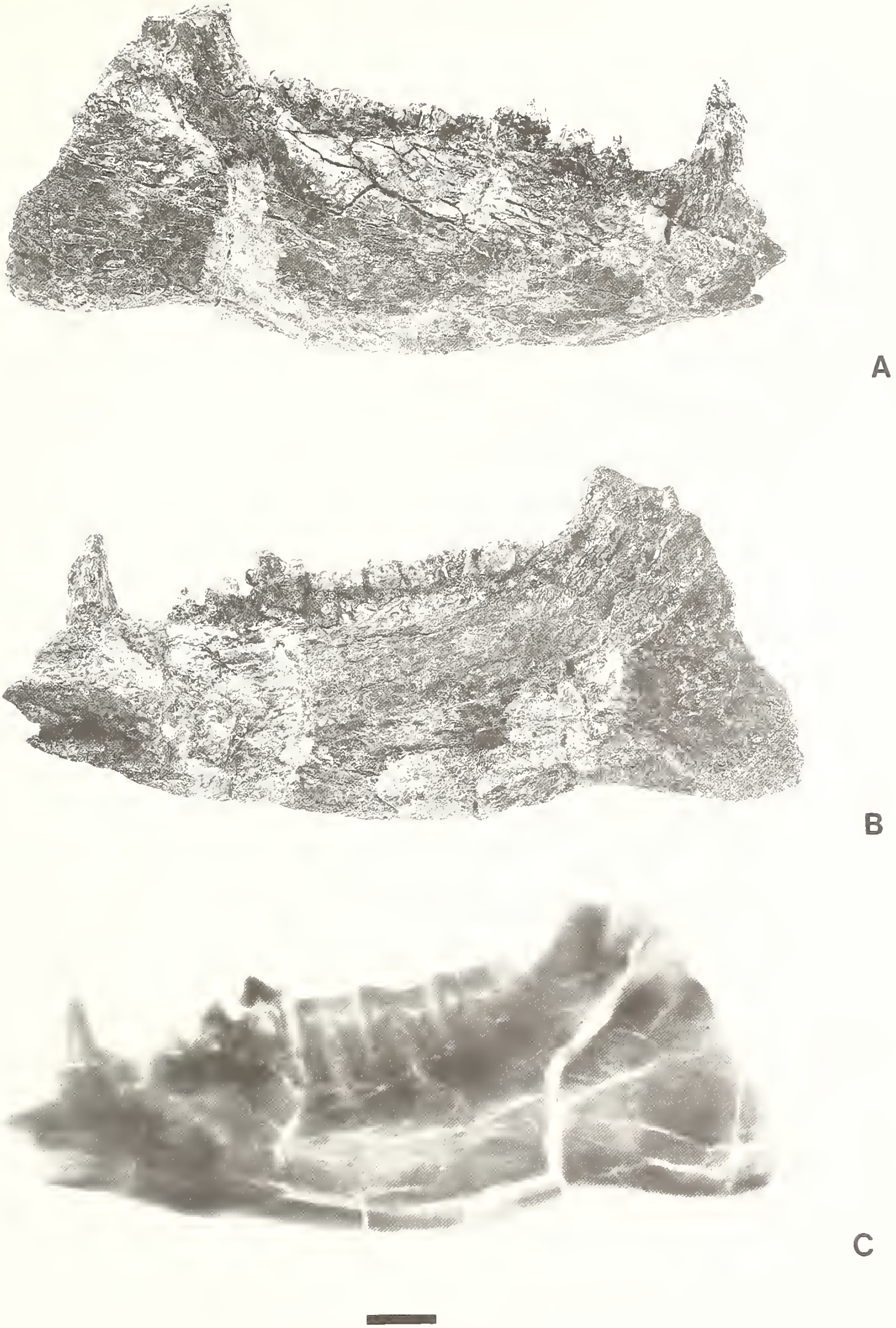
All upper molars display the same pattern (Text-figs 1, 2a–b). They consist of four main cusps, more or less pyramidal in shape, the labial ones laterally more compressed and slightly more mesial in position than the lingual ones. The paracone is the highest cusp. Two mesial and distal enamel swellings, scarcely differentiated as accessory cusps, recall the upper molars of the North American genus *Perchoerus* Leidy, 1869. The mesial swelling occurs between the two anterior main cusps and is close to the labial face of the protocone. The distal swelling occurs between the two posterior main cusps and is close to the mesiolabial face of the hypocone. The cingulum occurs on all sides of the molars except the lingual side. The typical system of grooves in suoids (= 'Furchenplan' of von Hünermann, 1968) is only weakly expressed (tooth dimensions in Table 1).

TABLE 1. Dental dimensions of *Egatochoerus jaegeri* gen. et sp. nov. (all measurements are in mm).

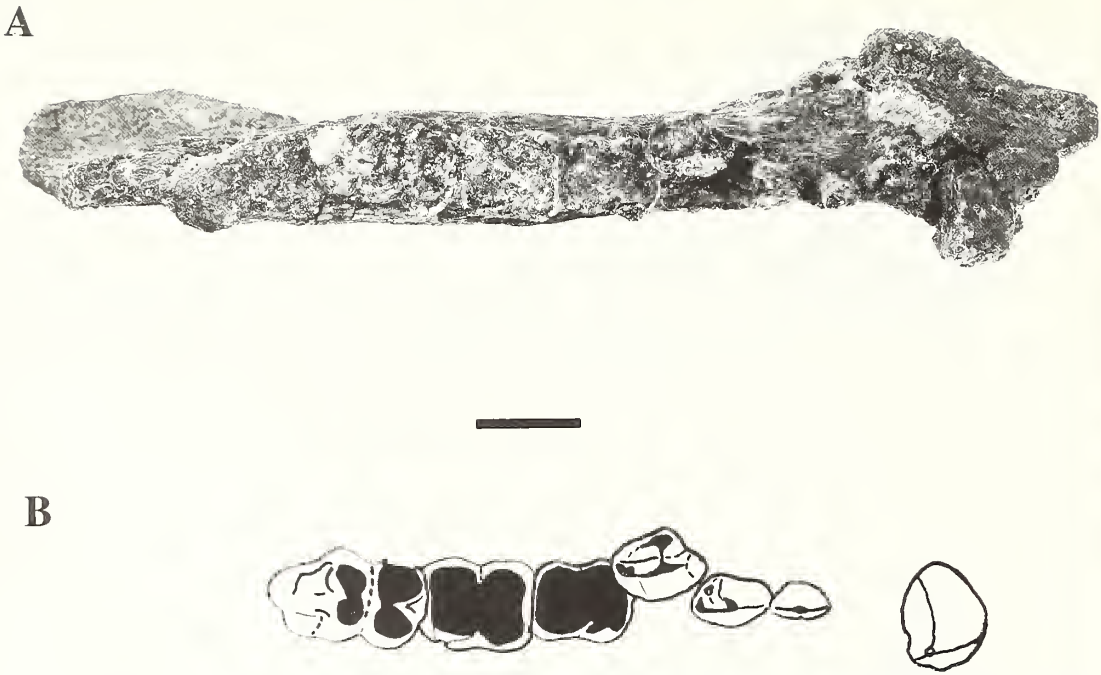
		Length	Width
TF 2672	rM1/	9·5	9·3
	rM2/	10·5	11·3
TF 2673	rM1/?	10·1	–
TF 2674	rM1/	9·9	–
TF 2681	r Canine	15·7	7·5
	rP/2	5·5	2·9
	rP/3	7·0	3·8
	rP/4	8·0	5·0
	rM/1	9·0	7·0
	rM/2	10·1	7·8
	rM/3	13·4	8·1
TF 2825	lP/3	6·7	4·1
	lP/4	8·4	5·9
	lM/1	9·0	6·7
	lM/2	9·5	8·2
	lM/3	13·8	8·7
TF 2827	lM2/	10·6	10·5
TF 2826	lDP4/	8·5	7·9
TF 2967	lI/2	5·8	5·5
TF 2968	rI/3	2·7	4·2
TF 2969	rI1/	4·4	7·1

The mandible is deep and massive (Text-fig. 3), but its depth decreases from P/3 anteriorly. The symphysis is low and extends distally as far as the mesial side of P/3. The angular process is strong, and salient downwards behind M/3, but not as downwardly salient as in *Perchoerus*. The ascending ramus is almost vertical and rises just behind M/3. There is no retromolar space.

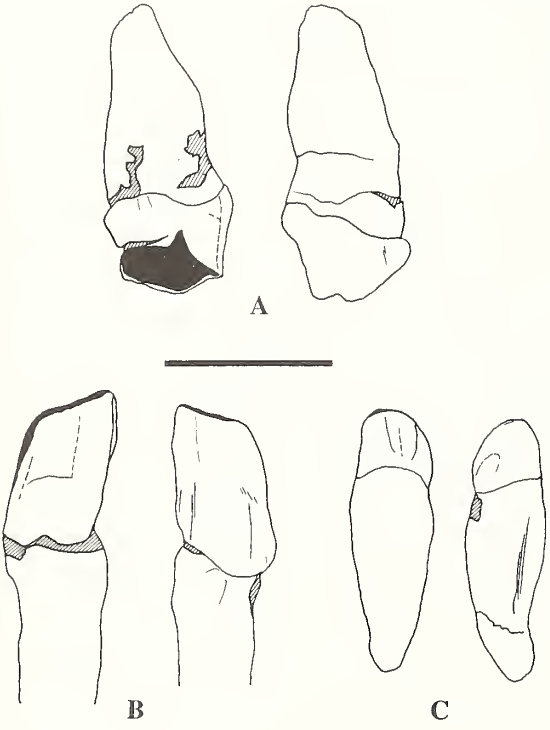
The lower canine is triangular in section (Text-fig. 4) and of *verrucosa* type (labial and lingual face about the same length and forming an acute angle of about 45°, according to the nomenclature proposed by Stehlin 1899–1900, p. 229). It is high, massive and vertical, and its insertion in the lower jaw is not marked by an outwards splaying of the bone, as is the case in many Suidae (Pickford 1988). Based on the reduced size of P/2, the P/1 is probably lost, which is confirmed by the absence of visible roots and alveoli in the radiographs of the specimen (Text-fig. 3c). However, the bony regions between the canine and P/2 are crushed, and it is difficult to be certain. The size of lower premolars increases from P/2 to P/4. The P/2 is damaged, and only parts of dentine and enamel are visible; but this tooth is small, with one root, and separated from the canine by a short diastema (about 8 mm). P/3 and P/4 are double-rooted and they display a well developed talonid. The P/4 is broad, with two main cusps (protoconid and metaconid) and displays a small mediolingual paraconid linked to the protoconid by a weak crest. The protoconid is slightly mesial to the metaconid, and a well developed hypoconid occurs on the labial side of the talonid (Text-fig. 2c–e; dimensions Table 1).



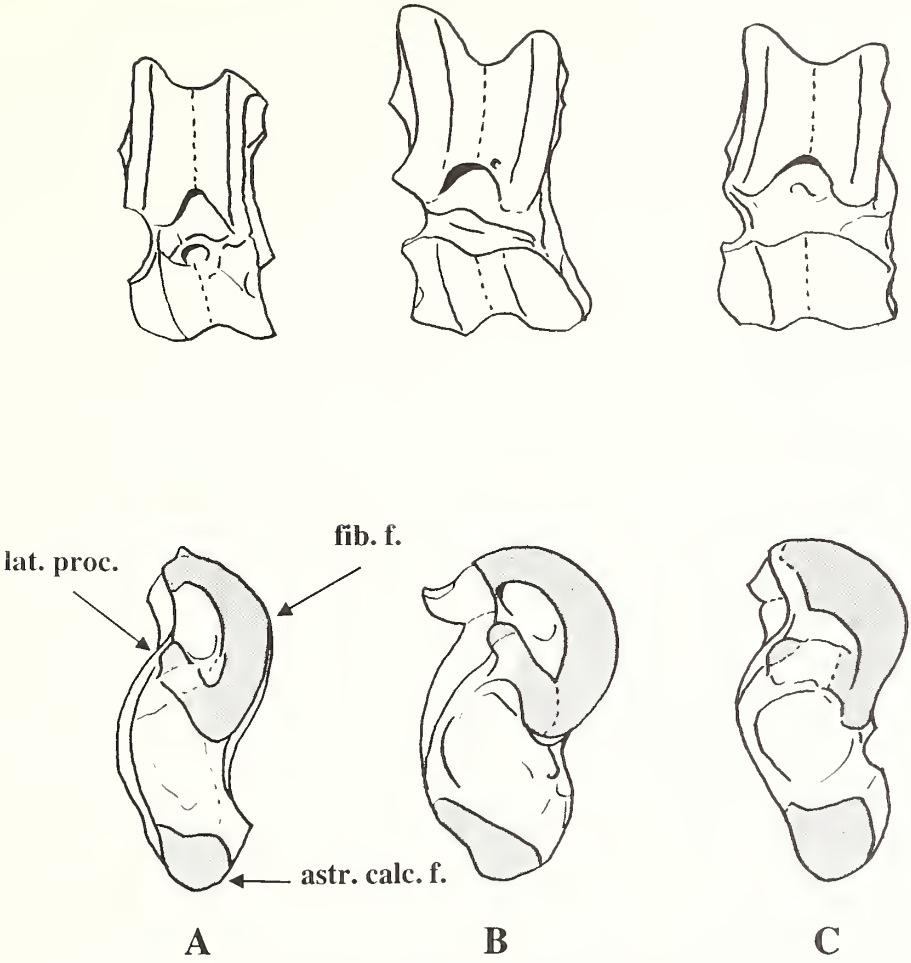
TEXT-FIG. 3. *Egatochoerus jaegeri* gen. et sp. nov. TF 2681; right lower jaw with canine and P/2-M/3; Bang Pu Dam, Thailand; upper Eocene. A, labial view; B, lingual view; C, lingual radiograph. Scale bar = 10 mm.



TEXT-FIG. 4. *Egatochoerus jaegeri* gen. et sp. nov. Bang Pu Dam, Thailand; upper Eocene. A, TF 2681; right lower jaw with canine and P/2-M/3, occlusal view. B, interpretative drawing of the same specimen. Scale bar = 10 mm.



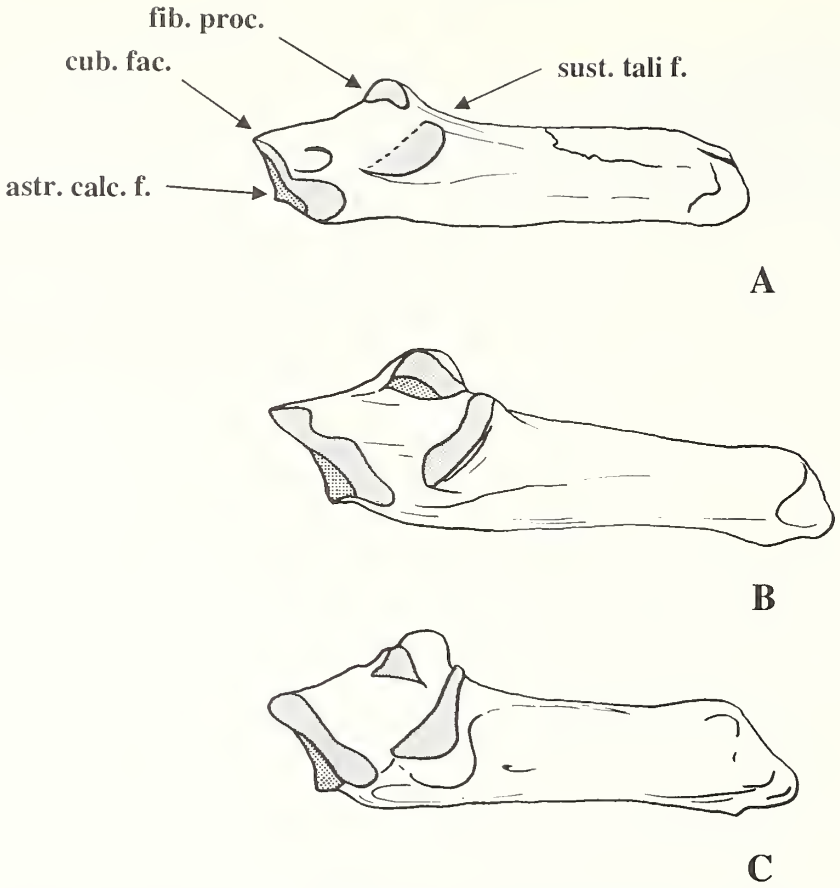
TEXT-FIG. 5. *Egatochoerus jaegeri* gen. et sp. nov. Bang Pu Dam, Thailand; upper Eocene. A, TF 2969; right I1/ in lingual (left) and labial (right) views. B, TF 2967; left I/2 in lingual (left) and labial (right) views. C, TF 2968; right I/3 in lingual (left) and labial (right) views. Scale bar = 10 mm.



TEXT-FIG. 6. Comparison of astragali of A, *Egatochoerus jaegeri* gen. et sp. nov. (TF 2812); B, *Doliochoerus quercyi*, inversed (GAR 480, Collections of the Laboratoire de Paléontologie de Montpellier II); and C, extant *Tayassu*. Upper line shows dorsal views, lower line lateral views. The bones are shown at about the same scale. Abbreviations: lat. proc. = lateral process on the dorsolateral side of the bone; fib. f. = fibular facet; astr. calc. f. = astragalo-calcaneal facet.

The lower molars are strongly worn, but on the lingual side of the teeth it is possible to distinguish two mesial and distal lobes separated by a deep groove. In addition, the four main cusps (protoconid, metaconid, hypoconid and entoconid) seem to be associated with small accessory crests but no additional cusps. The size of the lower molars increases from M/1 to M/3, and on the latter, the hypoconulid displays a third distal lobe narrower than the anterior ones (Text-fig. 4; dimensions Table 1).

The lower incisors are relatively small and their morphology indicates that they were probably emerging almost horizontally from the mandible. I/2 displays a narrow, rectangular and linguolabially compressed crown. Its lingual face shows a slight basal swelling of the enamel, and its labial face is almost flat. Its root is rectilinear and is about three times the length of the crown. The morphology of I/2 recalls those of *Perchoerus* and *Tayassu* (Text-fig. 5B). I/3 is reduced, as in *Perchoerus*, conical, and its crown is slightly linguolabially compressed. Its labial face is somewhat convex, and there is no basal swelling on its lingual face. Its root is very short (Text-fig. 5C). I1/ is obliquely worn by the abrasion of I/1. The crown is labiolingually compressed and the root is short but broad. The lingual face is slightly concave with a groove running from the apex of the crown to its base. Mesially, this groove is limited by a sharp edge with a small basal swelling of the enamel.



TEXT-FIG. 7. Comparison of internal view of calcanei of A, *Egatochoerus jaegeri* gen. et sp. nov. (TF 2814); B, *Doliochoerus quercyi* (GAR 459, Collections of the Laboratoire de Paléontologie de Montpellier II); and C, extant *Tayassu*. The bones are shown at about the same scale. Abbreviations: fib. proc. = fibular process; astr. calc. f. = astragalo-calcaneal facet; cub. fac. = cuboid facet; sust. tali f. = facet for the *sustentaculum tali*.

The labial face is very slightly concave, and the crown does not have serrate cutting edges, as in *Perchoerus* (Text-fig. 5A; dimensions Table 1).

Among the postcranial material found in association with the dental remains, two astragali and a calcaneum can be attributed to *Egatochoerus*.

The astragalus of *Egatochoerus* is slender, with the proximal trochlea wider and longer than the distal one. The distal trochlea is rotated medially with respect to the proximal trochlea. The sagittal ridge on the distal trochlea is sharp. The sustentacular facet is mediolaterally convex and occupies the whole width of the plantar face. A very slight ridge occurs on the medial side of the sustentacular facet. In lateral view, an articular facet corresponding to the fibula runs along the whole anterior part of the proximal trochlea. The facet joins a small lateral process on the dorsolateral side of the bone that articulates with the fibular process of the calcaneum. Distally, a large facet occurs and articulates with the anteromedial part of the calcaneum (Text-fig. 6).

The calcaneum is slender with a laterally compressed *processus calcanei*. On its distal end, it inflates as a bilobed process (*tuber calcanei*) that is divided by a slight groove (*flexor digitalis pedis superficialis*). Medially, the *sustentaculum tali* is massive and displays a somewhat circular articular facet for the sustentacular facet of the astragalus. On the dorsal face of the calcaneum, the fibular process is short and it displays on its anterior edge a flat articular surface for the fibula. On its medial side, a kidney-shape facet corresponds to the small lateral process of the lateral face of the astragalus. On the anterior side of the calcaneum, a narrow elongated facet articulates with the cuboid. This facet displays an angle of about 50° with the *processus calcanei*. An

TABLE 2. Dimensions of postcranial elements of *Egatochoerus jaegeri* gen. et sp. nov. LH = lateral height; TDDT = transverse diameter of the distal trochlea; TDPT = transversal diameter of the proximal trochlea; TH = total height; TDPC = transverse diameter of the *processus calcanei*; TDST = transverse diameter of the *sustentaculum tali*; HFP = height of the fibular process (all measurements are in mm).

Astragalus	LH	TDDT	TDPT	
TF 2812	23·3	10·5	10·5	
TF 2813	23·6	10·6	10·8	
Calcaneum	TH	TDPC	TDST	HFP
TF 2814	41·9	6·0	9·8	4·4

anteromedial facet articulates with the lateral part of the distal trochlea of the astragalus. The ventral side of the calcaneum somewhat inflates under the *sustentaculum tali* and the fibular process (Text-fig. 7).

COMPARISONS

In the present work, *Egatochoerus* will be compared with the European genera *Propalaeochoerus*, *Palaeochoerus*, *Doliochoerus*, the North American genus *Perchoerus* and the Chinese genus *Odoichoerus* because these Palaeogene suoids display morphologies close to that of the form described here. In addition, postcranial material will also be compared with that of *Doliochoerus* and of extant *Tayassu*. The main characters of the principal genera discussed in the text are shown in Table 3.

Propalaeochoerus. The mandible of *Propalaeochoerus* is much shallower than that of *Egatochoerus*, with a fused symphysis and a very weak angular process. In addition, *Egatochoerus* differs from *Propalaeochoerus* and *Palaeochoerus* in its P/4 with weaker hypoconid and entoconid, less well developed paraconid, protoconid less mesial to the metaconid and talonid slightly narrower than trigonid. In *Egatochoerus*, the lower molars are more square in occlusal view, and the waist between the two lobes is much deeper. The upper molars of *Egatochoerus* are slightly more square with narrower mesial and distal cingulum.

Palaeochoerus. The European species of *Palaeochoerus* differ from *Egatochoerus* in their larger size, their upper molars with stronger labial cingula and with lingual cingula (in *P. typus* Pomel, 1847 for example), with a more reduced metaconule, indistinct mesial and distal accessory cusps, less bulbous cusps and in their more slender mandible.

Doliochoerus. According to Ginsburg (1974, p. 60), *Doliochoerus quercyi* possessed a P/4 recalling the lower carnassial tooth of a carnivore, with its reduced metaconid, and the protoconid linked by a crest to a lingual and well expressed paraconid. This structure is also observed in *Egatochoerus*. However, it must be stressed that the lower canine in *Egatochoerus* is less curved, and that its internal and external faces form a more open angle than in *Doliochoerus quercyi*. In addition, the increasing size of lower premolars is more pronounced in *Egatochoerus*, its mandible is deeper, and the depth of its horizontal ramus increases backwards. The upper molars of *Doliochoerus* are also more bulbous, the accessory cusps are smaller and hidden in crests, and its P4/ is better developed. Finally, the two species of the European genus are larger than *Egatochoerus*.

Despite these differences, several derived characters are shared between *Doliochoerus* and *Egatochoerus*: general structure of the molars, P/4 with bifid apex and distinct paraconid and talonid, occurrence of a small talonid on P/3 and symphysis reaching P/3. However, *Egatochoerus* also displays a more conservative condition than *Doliochoerus* by its less developed P/4, its upper molars with weaker crests, its less molarized P4/ and by its smaller size.

Perchoerus. The North American *Perchoerus* is known from the middle Chadronian (upper Eocene, see Stucky 1992) to the Whitneyan (middle Oligocene). This genus differs mainly from

TABLE 3. Comparative table of the main characters of the principal genera discussed in the text.

	Egatochoerus	*Dolichoerus*	*Perchoerus*	*Propalaeochoerus*	*Palaeochoerus*	*Tayassu*
Mandible	Deep	Shallow	Deep	Shallow	Shallow	Deep
Deepness of mandible decreases anteriorly	Yes	No	Yes	No	No	Yes
Angular process downwardly salient	Yes	No	Yes	No	No	Yes
Lower canine vertical	Yes	No	Yes	Yes	Yes	Yes
P/1	Lost	Retained	Retained	Retained	Retained	Lost
P/4 talonid	Weakly developed	Strong	Strong	Strong	Strong	Strong
Position of paraconid on P/4	Low	High	Low	High	High	High
P/4 talonid narrower than trigonid	Yes	Same width	Yes	Talonid wider than trigonid	Same width	Same width
Size reduction of premolars anteriorly	Strong	Weak	Strong	Weak	Weak	Strong
Sulcus between lobes of lower molars	Deep	Weak	Deep	Weak	Weak	Weak
Width of first and second lobes of M/3	1st = 2nd	1st > 2nd	1st > 2nd	1st > 2nd	1st > 2nd	1st > 2nd
Lingual cingulum on P4/	No	Yes (weak)	Yes (weak)	Yes (strong)	Yes (weak)	No
Occlusal outline of upper molars	As long as wide	Wider than long	Wider than long	Wider than long	Wider than long	As long as wide
Labial cingulum of upper molars	Weak	Strong	Strong	Strong	Strong	Strong
Accessory cusps on upper molars	Two, distinct	Fused in crests	Three, distinct	Fused in crests	Fused in crests	Fused in crests
Lingual roots of upper molars	Fused	Fused	?	Fused	Distinct or fused (1)	Distinct

TABLE 3. Comparative table of the main characters of the principal genera discussed in the text.

	Egatochoerus	*Doliochoerus*	*Perchoerus*	*Propalaeochoerus*	*Palaeochoerus*	*Tayassu*
Mandible	Deep	Shallow	Deep	Shallow	Shallow	Deep
Deepness of mandible decreases anteriorly	Yes	No	Yes	No	No	Yes
Angular process downwardly salient	Yes	No	Yes	No	No	Yes
Lower canine vertical	Yes	No	Yes	Yes	Yes	Yes
P/1	Lost	Retained	Retained	Retained	Retained	Lost
P/4 talonid	Weakly developed	Strong	Strong	Strong	Strong	Strong
Position of paraconid on P/4	Low	High	Low	High	High	High
P/4 talonid narrower than trigonid	Yes	Same width	Yes	Talonid wider than trigonid	Same width	Same width
Size reduction of premolars anteriorly	Strong	Weak	Strong	Weak	Weak	Strong
Sulcus between lobes of lower molars	Deep	Weak	Deep	Weak	Weak	Weak
Width of first and second lobes of M/3	1st = 2nd	1st > 2nd	1st > 2nd	1st > 2nd	1st > 2nd	1st > 2nd
Lingual cingulum on P4/	No	Yes (weak)	Yes (weak)	Yes (strong)	Yes (weak)	No
Occlusal outline of upper molars	As long as wide	Wider than long	Wider than long	Wider than long	Wider than long	As long as wide
Labial cingulum of upper molars	Weak	Strong	Strong	Strong	Strong	Strong
Accessory cusps on upper molars	Two, distinct	Fused in crests	Three, distinct	Fused in crests	Fused in crests	Fused in crests
Lingual roots of upper molars	Fused	Fused	?	Fused	Distinct or fused (1)	Distinct

Egatochoerus in its larger size, the retention of P/1, and by the slightly longer talonids of its P/3 and P/4. The common features shared by *Egatochoerus* and *Perchoerus* (molar and premolar structure, morphology of the mandible) suggest a close relationship between the two taxa. However, *Egatochoerus* is more primitive than *Perchoerus* in having a slightly less molarized P/4 and by the less developed diastema in the lower premolar row. On the other hand, the loss of P/1 in *Egatochoerus* indicates a more advanced condition for the Asian form.

The systematic position of Odoichoerus uniconus *Tong and Zhao, 1986*

The fragmentary mandible attributed to *Odoichoerus uniconus* from the lower Oligocene of China (Tong and Zhao 1986) differs strongly from *Egatochoerus* in its much shallower horizontal ramus, its narrower lower molars with better developed talonid, yet with extremely reduced hypoconulid on M/3 and mainly by the structure of its P/4, which is a very simple, triangular and sharp tooth. The Chinese species, as suggested by Tong and Zhao (1986), appears to be closer to Neogene forms such as *Taucanamo* and *Albanohyus* by the very primitive morphology of its P/4. However, *Taucanamo* is larger, its lower molars are much more complex, and its P/4 is sharp and made up of only one main cusp. The latter character suggests a position for *Odoichoerus* outside the family Tayassuidae which is characterized, among other features, by the presence of a more molarized P/4. The dental and mandibular morphologies of the Chinese species warrant an attribution to the family Suidae.

Postcranial skeleton

The postcranial elements of *Egatochoerus* permit comparisons with the genera *Doliochoerus* and *Tayassu*, the astragalus of *Perchoerus* being unknown.

The astragalus of *Egatochoerus* is slender, with the proximal trochlea wider and better developed than the distal trochlea, whereas the latter is about the same width as the proximal trochlea in the other two genera (Text-fig. 6). The astragali of *Egatochoerus* and *Tayassu* are about the same height, but in *Tayassu* this bone is wider and more massive. The axes of the proximal and distal trochleae are in a slightly more open angle in *Tayassu* than in *Egatochoerus* and *Doliochoerus*. On the other hand, the gulley of the proximal trochlea is wider in *Tayassu* and *Egatochoerus* than in *Doliochoerus*. In these three taxa, the articular facet for the cuboid is reduced and narrower than that for the navicular. Moreover, the groove between these two facets is much more marked in *Tayassu* and *Egatochoerus* than in *Doliochoerus* in which this surface is rather flat. The astragalus of *Egatochoerus* thus displays a morphology slightly closer to that of *Tayassu* (dimensions Table 2).

The proportions of the calcanei are similar in the three forms. The major difference is the occurrence of a posteroventral extension of the *sustentaculum tali* in *Tayassu*, which is absent in the fossil taxa (Text-fig. 7). This structure also displays an almost circular articular facet in all three genera (dimensions Table 2). One can also observe that the orientation of the facet for the *sustentaculum tali* becomes more vertical from *Egatochoerus* to *Tayassu*. This can be correlated with the articulation between the astragalus and the calcaneum and thus with the position of the hind limb which displays a more acute angle between the tibia and the metapodials in *Egatochoerus* and a more open angle between these two elements in *Tayassu*. The hind limb of *Egatochoerus* was probably less erected than that of *Tayassu*. In addition, it must be stressed that the fibular process is better developed from *Egatochoerus* to *Tayassu*, suggesting that the posterior limb of *Tayassu* is more limited in its lateral motions than that of *Doliochoerus* and *Egatochoerus*.

Among the tarsal bones, both the astragali and the calcanei display diagnostic characters discriminating the different genera. The structure of these bones varied considerably during evolution according to the constraints linked to body weight, the motions of the posterior limb and thus to adaptations for different displacements of these bones.

DISCUSSION

Dental characters in Tayassuidae

It must be stressed that the distinction between the two families Tayassuidae and Suidae is unclear. The genus *Palaeochoerus*, the familial status of which has been diversely interpreted, is a typical example of this, as Pickford (1988) has recently pointed out. Indeed, Viret (1961) classified this genus among the Suidae, Ginsburg (1974) included it in Tayassuidae, while Pickford (1988) returned it to the Suidae and created the subfamily Palaeochoerinae. Finally, Hellmund (1992) referred the genera *Palaeochoerus* and *Propalaeochoerus* to the Tayassuidae. According to Pickford, the subfamily Palaeochoerinae is the most ancient among the Suidae, and closely related to the Tayassuidae, based on retention of numerous primitive characters in this group. As Pickford claimed, the systematic position of *Palaeochoerus* depends on the choice of characters. In addition, he made the Tayassuidae the stem-group of the Suoidea in his proposed cladogram (1988, p. 10).

Most of the dental characters proposed by Pickford (1988) to define the Palaeochoerinae are primitive and can also apply to the Tayassuidae. In addition, Pickford gave a list of characters of the base of the skull; these unfortunately are impossible to compare with the Thai form. However, *Egatochoerus jaegeri* can be distinguished dentally from representatives of the subfamily by the presence of a marked diastema between the canine and P/2 and by the absence of a partial overlapping of the talonid of M/3 by the base of the ascending ramus.

Pickford and Morales (1989) compiled a list of dental and cranial characters that they considered typical of the family Tayassuidae and differentiating it from the Suidae: lower canine vertical and close to the lower premolars in the dental row, absence of symphyseal splaying of the lower jaw in the canine area (as is the case in Suidae), lower premolars in a closed series, strongly developed trigonid on P/4, gradual increase in size and complexity of the lower premolar crown morphology from front to rear, lower and upper molars lingually and labially poorly salient, system of grooves (= 'Furchenplan' of von Hünermann 1968) poorly expressed and rather thin enamel. It is possible to add two characters that Pickford and Morales did not give (but later cited by Pickford 1988, pp. 12, 13), namely the lower dental row which is not oblique in comparison with the longitudinal axis of the horizontal ramus (in Suidae, the dental row crosses over the body of the mandible from antero-labial to postero-lingual) and the weak linguo-labial thickness of the horizontal ramus (in Suidae, lower molars display very divergent roots, and the linguo-labial thickness of the horizontal ramus is important). These features also occur in *Egatochoerus*, *Perchoerus* and the extant *Tayassu*, in addition to a downward and backward salient angular process of the mandible, the anteriorly shallowness of the horizontal ramus, the shallow symphysis and the absence of a retromolar space behind M/3. This suggests an immediate phylogenetic relationship between the Asiatic form and *Perchoerus*. Indeed, *Egatochoerus* seems to have more affinities with the North American genus than with any other known taxon from the Old World. *Egatochoerus* is more primitive than *Perchoerus* and is characterized by numerous conservative features (morphology of the angular process and of the P/4, P4/ without lingual cingulum, upper molars with poorly defined accessory cusps and without lingual cingulum,...), which indicate that the origin of the Suoidea, and probably the Suidae, is rooted among the Tayassuidae. On the other hand, the difficulties encountered in establishing a set of derived characters for the Tayassuidae that allows us to distinguish them from the Suidae illustrate the close relationships that exist between the two families. Among these characters, one can cite the early molarization of P/4, and later that of P/3. This molarization began as early as the late Eocene, as displayed by the lower jaw of *Egatochoerus*, and possibly earlier in Tayassuidae, because Suidae are characterized by an increasing chewing surface on molars. A process of reversion in the molarization of the lower premolars in Suidae that occurred from the Miocene can thus be envisaged.

The tayassuid–hippopotamid relationships

Pickford (1989) suggested that hippopotamids could have originated from an Old World peccary stock. As part of this theory, he proposed that if the lineage of hippopotamids could be traced back to the Oligocene tayassuid *Doliochoerus*, the unknown ancestor of *Doliochoerus* might be found among the Cebochoeridae (an Artiodactyl family known exclusively from the Eocene of Europe), as suggested by Pearson (1927). Observation of the dental morphology of the Cebochoeridae indicates that there is probably no relationship between them and *Doliochoerus*. Indeed, the Cebochoeridae differ from the Suidae and Tayassuidae in their upper molars with labial cusps linked by a crest and with lingual cusps that tend to be selenodont, a two-rooted upper canine, lower molars with crescentiform labial cusps, a caniniform P/1 and in their incisiform lower canine. The similarities that may have occurred between the two groups can be considered only as convergences, and the hypothesis proposed by Pickford (1989) is therefore less likely. It is more logical to derive *Doliochoerus* from less specialized forms such as the Chinese *Odoichoerus* which displays a primitive suid morphology.

Biogeographical hypothesis of the family Tayassuidae during the Palaeogene

It is not yet possible to demonstrate that the Krabi mammal fauna is certainly older than the North American localities that have yielded the oldest remains of *Perchoerus*, but several lines of evidence argue for such a conclusion. The first occurrence of *Perchoerus* in North America is estimated to be at about 36–35 Ma (middle Chadronian according to Stucky 1992). However, an age comprised between 40 and 35 Ma (late Eocene) has been proposed for Krabi (Ducrocq *et al.* 1991). In addition, the anthracotheres associated with *Egatochoerus* in Krabi display a dental morphology intermediate between that of the upper Eocene taxa from Pondaung in Burma and that of the anthracotheres from the basal Oligocene of Monteviale in Italia (Ducrocq *et al.* 1992; Ducrocq 1994). The dental morphology of the anthracotheres from Central Europe, radiometrically dated from about 37 Ma (Fejfar 1987), is nearly identical with that of the forms from Thailand and suggests that a similar age could be envisaged for the Krabi fauna (Ducrocq 1994). In addition, the occurrence of the most primitive known anthracothere *Siamotherium krabiense* in Krabi (Suteethorn *et al.* 1988, Ducrocq *et al.* 1992) strongly argues for an early late Eocene age for the mammalian association from Thailand. Finally, given the evolutive degree of both *Egatochoerus* and *Perchoerus*, it is possible to suppose that the Asian form is slightly older than the North American taxon.

The earliest known representative of the family Tayassuidae (*Egatochoerus jaegeri*) appeared in the late Eocene of South East Asia (South Thailand). This form migrated into North America during the late Eocene and gave rise to *Perchoerus* which locally radiated up to the middle Oligocene (Whitneyan). The Oligocene evolution of North American tayassuids took place, apparently without influence from the Old World taxa, and the North American peccaries never left the New World after their first arrival there. On the basis of the present fossil record, *Egatochoerus* cannot be related directly to other Asian suoids, and it could be suggested that the Thai species became extinct in Asia without leaving descendants. Another migration occurred from Asia into Europe during the late Eocene or the early Oligocene, but it cannot yet be determined if *Egatochoerus* was at the origin of this migration, given the poor fossil record of Palaeogene tayassuids. The Oligocene genera *Doliochoerus*, *Propalaeochoerus* and *Palaeochoerus* 'suddenly' appeared in western Europe without known direct ancestors. The tayassuids evolved in Europe and Asia up to the late Miocene. On the basis of their dental and mandible morphologies, it is unlikely that the European Palaeogene tayassuids derived from an ancestor such as *Egatochoerus*. The direct ancestry of the European taxa should be investigated among conservative forms resembling the Chinese *Odoichoerus*.

CONCLUSIONS

Egatochoerus jaegeri from the upper Eocene of Thailand is the oldest known member of the Tayassuidae, and its affinities with the North American genus *Perchoerus* confirm that faunal exchanges were possible in Asia and North America at least during the late Eocene. The migration probably occurred from Asia to the North American landmass given the more archaic condition of the Thai specimen with respect to the New World form, and a South East Asian origin for the tayassuids seems actually well established. The ancestor of the European tayassuids *Doliochoerus*, *Propalaeochoerus* and *Palaeochoerus* is unknown at present but it could be sought in a form more conservative than *Egatochoerus*. In addition, the Chinese species *Odoichoerus uniconus* is tentatively removed from the Tayassuidae mainly on the basis of its P/4 morphology, and is referred to the Suidae.

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THE APPARATUS ARCHITECTURE OF *PANDERODUS* AND ITS IMPLICATIONS FOR CONIFORM CONODONT CLASSIFICATION

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ABSTRACT. The apparatus composition and architecture of the coniform conodont genus *Panderodus* (Llanvirn–Givetian) has been reconstructed from a bedding plane assemblage associated with soft parts from the Waukesha lagerstätte of Wisconsin, together with published clusters and discrete element collections. This modelling enables a redefinition of the apparatus and species concepts within *Panderodus*, which is now reconstructed as a nonimembrate apparatus, with four subdivisions in the graciliform element category. Architecturally the apparatus falls into three locational domains. The architecture of panderodontid conodonts confirms their status as a distinct ordinal-level group. Extrapolating this architectural model, it has been possible to recognize recurrent apparatus styles within non-panderodontid coniform genera such as *Besselodus* and *Dapsilodus*, lending a firm basis to their suprageneric classification.

THE mineralized oral apparatus is the only commonly preserved part of conodonts, usually as discrete elements in acid residues. The reconstruction of apparatuses from discrete elements provides the basis for a multielement taxonomy and any subsequent palaeobiological work. Features used for reconstruction include common co-occurrence and stratigraphical range, morphological similarities between elements, and comparison with templates provided by previously reconstructed apparatuses and natural assemblages. No attempt is made to reconstruct individuals, but rather to document the range of variation within a given species, independent of age, sex or any other individual factor (Smith *et al.* 1987). Multielement taxonomy has led to a number of major advances in rationalizing the classification and phylogeny of conodonts (Sweet 1988).

The discovery of the Granton conodont specimens with associated soft tissues (Briggs *et al.* 1983) has led to a number of papers (Aldridge *et al.* 1986, 1993; Aldridge 1987; Aldridge and Briggs 1986, 1989; Conway-Morris 1989) which have shown these ozarkodinids to be laterally compressed, some 40 mm long with caudal fins, a well-developed myomeric musculature, notochord and eyes. These animals are presumed to have been active, predatory, nektobenthonic, primitive chordates. The identification of cellular bone, enamel homologues and cartilage in conodont elements has confirmed the vertebrate nature of conodonts (Sansom *et al.* 1992).

Jeppsson (1971) produced a model of element arrangement in *Ozarkodina* Branson and Mehl apparatuses based upon isolated clusters and numerical methods. Work on the Granton animals and bedding plane assemblages (Aldridge *et al.* 1987) largely confirmed Jeppsson's model but, in addition, Aldridge *et al.* (1987) proposed a food gathering and processing function for the ozarkodinid apparatus. The anterior 'ramiform' basket was postulated to have a grasping function and the posterior pectiniform complex a slicing and grinding role. This model has been supported by detailed morphological analyses which propose a tooth-like function for the individual elements (Jeppsson 1979; Purnell and von Bitter 1992; Purnell 1993).

Although substantial advances have been made in reconstructing coniform apparatuses since the first attempts of Webers (1966) and Bergström and Sweet (1966), two major problems remain. Firstly, coniform elements show subtle changes in morphology, particularly in large collections, and it is often very difficult to reconstruct coniform apparatuses and distinguish between inter- and intra-specific characters. Secondly, there are few natural assemblages or diagenetic clusters with

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which to confirm apparatus reconstructions. With the discovery of a number of diagenetically fused clusters of the genus *Panderodus* Ethington (An *et al.* 1983; Kozur 1984; Balogh and Kozur 1985; Dzik and Drygant 1986), and the description of a *Panderodus* bedding plane assemblage with associated soft parts from the Silurian Konservat Lagerstätte of Waukesha, Wisconsin, USA (Smith *et al.* 1987), sufficient data are now available to refine the architectural and functional model for the *Panderodus* apparatus proposed by Smith *et al.* (1987). This is particularly pertinent as there is evidence that species of *Panderodus* had a pelagic rather than nektobenthic mode of life (Barnes, Rexroad and Miller 1973; Barnes and Fåhræus 1975; LeFèvre *et al.* 1976; Aldridge and Mabillard 1981). Additionally, there is some equivocal soft part evidence that suggests they may have had a fundamentally different body plan to that of ozarkodinid species, being dorsoventrally, rather than laterally, flattened (Smith *et al.* 1987; Conway-Morris 1989).

The architectural model presented offers the potential of simplifying the nomenclatural morass that has developed in *Panderodus* taxonomy, allowing a more precise biological diagnosis of constituent species.

DEVELOPMENT OF THE GENERIC AND SPECIES CONCEPT IN *PANDERODUS*

Bergström and Sweet (1966) produced the first multielement reconstruction of *Panderodus*. They recognized *Panderodus gracilis* (Branson and Mehl) as a bielemental apparatus (Text-fig. 1) which comprised a slender, elongate element (*P. gracilis* (Branson and Mehl)), and a laterally compressed element (*P. compressus* (Branson and Mehl)).

Bergström and Sweet 1966	*Cooper 1975, 1976*	*Barnes 1977*	*Barrick 1977*	*Sweet 1979*	*Barnes et al. 1979*	*Nowlan and Barnes; McCracken and Barnes 1981*
P gracilis	costate	narrow		arcuatiform	p	arcuatiform
			Sb	asimiliform		graciliform
			Sa	similiform		
P. compressus	simplexiform	wide	M	falciform	q	compressiform
			Sc	tortiform		

Fåhræus and Hunter 1985	*Dzik and Drygant 1986*	*Nowlan and McCracken (in Nowlan et al.) 1988*	*Jeppsson * 1983, 1989*	*Armstrong 1990*	*This Study descriptive*	*This Study locational*
D	hi	a/b	u	aq	**arcuatiform**	**qa**
C	ke/pl/tr/oz	b			**asym. graciliform**	**qg**
		c		sym. p	**sub-sym. graciliform**	**qg**
B	sp		ne	r	**truncatiform**	**qt**
A			tr		**aequaliform**	**ae**
E	ne	e	f	sq	**falciform**	**pf**
		a		tp	**tortiform**	**pt**

TEXT-FIG. 1. Terminology used by previous authors to describe the *Panderodus* apparatus, and the notation developed herein. Several authors have placed the same elements in different categories, providing a degree of confusion when applying our view of the *Panderodus* apparatus. (* Jeppsson has described some of the elements of *Panderodus* without illustration, but the senior author has had access to his collections, and correlation with other schemes is derived from his proposed homologies between this apparatus and that of *Belodella*).

A bielemental reconstruction was retained by Cooper (1975, 1976) who referred to simplexiform (= compressiform) and costate (= graciliform) elements (Text-fig. 1). Cooper did, however, suggest that further subdivisions could be made within the latter category. This was later formalized by Barrick (1977), who also tried to apply the nomenclature developed for ramiform-pectiniform apparatuses by Sweet and Schönlaub (1975). Barrick proposed that the compressiform element was homologous with the M element of ramiform-pectiniform apparatuses and the graciliform elements equivalent to the S elements of the first transition series; he gave no reason why the compressiform might not be a P ('platform') element.

Sweet (1979) considered the notational scheme applied to ramiform-pectiniform apparatuses to be inappropriate for coniform taxa, and applied a system based solely on the morphological character of *Panderodus* element (Text-fig. 1). The *Panderodus* apparatus proposed by Sweet (1979) was quinquemembrate, comprising three narrow-based costate elements (the asimiliform, similiform and arcuatiform), a laterally compressed falciform element (the compressiform or simplexiform of previous authors), and a small, twisted, tortiform element.

Barnes *et al.* (1979), in a review of Ordovician conodont genera, introduced a classification scheme specific to coniform apparatuses. They proposed several 'Types' which were defined upon the degree of elemental compression, cross-sectional symmetry and cusp curvature. *Panderodus* was described as a 'Type IIIB', bimembrate, apparatus, where cusp curvature was the most significant feature in delineating morphological transition between elements. In their notation scheme (Text-fig. 1) *Panderodus* comprised an erect p element (the graciliform) and a more highly recurved q element (the compressiform). Although oversimplified, this scheme had the advantage of allowing comparison of apparatuses without presupposing the homology of coniform and ramiform-pectiniform types.

Nowlan and Barnes (1981) suggested that three distinct apparatus types occur within species attributed to *Panderodus*. Group I, typified by *P. unicostatus* (Branson and Mehl), consisted of compressiform elements in association with a suite of variable graciliform and unicostate elements. Group II, included *P. gibber* Nowlan and Barnes, and was bimembrate with symmetrical and asymmetrical elements of similar general morphology. Group III, characterized by *P. liratus* Nowlan and Barnes, was also bimembrate, and divided into broad, laterally compressed, low-based elements, and long, slender, high-based elements.

Nowlan and McCracken (*in* Nowlan *et al.* 1988) applied the Barnes *et al.* (1979) scheme for ramiform-pectiniform apparatuses (Text-fig. 1), and modified the groupings to incorporate the discovery of additional elements. Group I panderodontids were quinquemembrate, with an a/b morphological transition series (Text-fig. 1), equivalent to the arcuatiform, asimiliform and tortiform elements, c subsymmetrical similiform elements. and the e falciform elements. Group II panderodontid apparatuses were trimembrate and consisted of a short unicostate a element, a symmetrical double furrowed c element, and a bicostate b element, similar in form to the a element. Group II apparatuses thus lacked the e (compressiform) element present in Group I species. Group III apparatuses were defined as bimembrate, with laterally compressed, broad, low-based elements (b/c) and long, slender a/b elements. Additional species, such as *Panderodus clinatus* McCracken and Barnes 1981 were found not to fit into any of the above groups.

Jeppsson (1983*a*, 1983*b*) mentioned the presence of eight to ten groups of homologous elements in each *Panderodus* species. Additionally, he implied locational homology between two of these element groups and those present in ozarkodinid apparatuses. One of these elements was totally symmetrical, unpaired and double-furrowed, and this he homologized with the tr element of Jeppsson (1971); the Sa of authors adopting Sweet and Schönlaub's (1975) terminology of other ramiform-pectiniform genera. Subsequently, Jeppsson (1989; Text-fig. 1) introduced a notation scheme for coniform taxa based upon reconstructions of *Belodella*. He proposed homology between certain elements in this apparatus and *Panderodus* species; namely, compressiform (f elements); unicostate, arcuatiform elements (u), symmetrical (tr) and short, twisted (ne) elements.

Fåhræus and Hunter (1985) recognized the presence of five morphological groupings in *Panderodus* apparatuses (Text-fig. 1). Group A consisted of symmetrical bi-furrowed elements, Groups B, C and D were described as asymmetrical 'gracilid' elements (similiform, asimiliform and arcuatiform *sensu* Sweet 1979), and Group E included 'compressid' elements. Additionally, Fåhræus and Hunter (1985) suggested that a curvature transition series occurred within each element type and they implied that the curvature transition was continuous; thus a very large number of elements could form each series and be present in each individual.

In their description of a diagenetically fused cluster of *Panderodus unicostatus* elements from the Ukraine, Dzik and Drygant (1986) recognized the presence of seven paired element morphotypes, and reconstructed the apparatus in the form of a bilateral size gradation. Discussing the problems of producing a standard notation, they implied homology with other apparatuses by the application of Jeppsson's (1971) scheme, and utilized the descriptive terminology developed for *Panderodus* by Sweet (1979; Text-fig. 1). However, they felt that the compressiform element, the largest present in the Podolia cluster, was locationally equivalent to the ne element, a notable departure from Jeppsson's (1983*a*, 1983*b*, 1989) view. This is based on their assumption that this element was located anteriorly in the apparatus. Dzik and Drygant (1986) also described a pair of tr elements, rather than a single one. Five pairs of graciliform elements were found in the cluster, and were described as arcuatiform (locationally the ke), similiform (pl and tr) and asimiliform (oz and sp, the latter was markedly shorter than the other forms). The unicostate pair were described as tortiform and homologized with hi elements. They suggested that, for practical purposes, 'it seems enough to distinguish only three easily recognizable element types. They may be denominated with location symbols as ne, hi, and ke–sp, respectively' (Dzik and Drygant 1986, p. 138).

Dzik (1991) redefined this locational homology, with the graciliform suite represented by pl–ke elements, and the oz elements being absent. In addition, homology between *Panderodus* and ramiform-pectiniform apparatuses was further pursued, despite Dzik's proposal that *Panderodus* possessed a distinctive 'chaetognath-type' apparatus, lacking a medial element and the 'pharyngeal' components of ramiform-pectiniform apparatus.

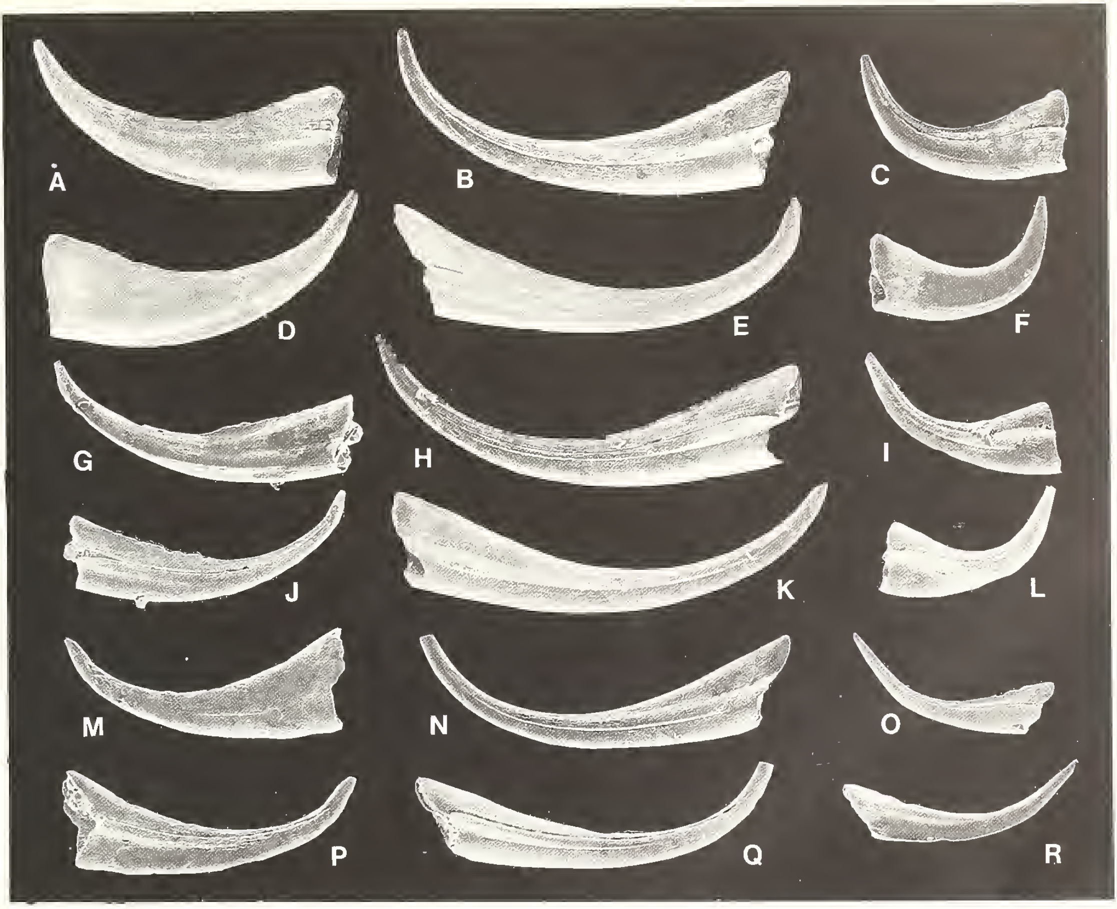
Armstrong (1990) expanded the Barnes *et al.* (1979) coniform scheme by subdividing the p and q categories using cusp cross-section (Text-fig. 1). The *Panderodus* apparatus thus contained sub-symmetrical and asymmetrical p and q elements, a tortiform tp element, and a short recurved r element. He considered the r element to be homologous with the oistodontiform element found in many Ordovician coniform taxa. Using this scheme, Armstrong (1990) proposed a homology of the elements in all Silurian coniform taxa, and suggested that this was the way forward in developing a suprageneric classification for coniform euconodonts.

COMPOSITION OF *PANDERODUS* APPARATUSES

In the following descriptions of *Panderodus* clusters, purely descriptive terms have been adopted. Six element morphotypes have been formalized in this study, although a further four sub-divisions within one element category have been recognized in isolated collections and natural assemblages of *Panderodus*. These categories are recognized on the basis of cusp curvature and cross-sectional symmetry. Eight are found as 'left' and 'right' pairs with single furrows on alternate lateral faces, whilst the ninth is symmetrical, furrowed on each lateral face and is thought to be unpaired. The major shape categories of Sweet (1979) have been modified and expanded, descriptive terminology largely follows Sweet (1981).

Falciform elements. (Text-fig. 2A, D) These have previously been described as simplexiform (Cooper 1975, 1976), compressiform (Nowlan and Barnes 1981; McCracken and Barnes 1981), ne (Dzik and Drygant 1986), e (Nowlan and McCracken *in* Nowlan *et al.* 1988), and f (Jeppsson 1989) elements (Text-fig. 1). In the type species, *Panderodus unicostatus*, these elements are characterized by gradually curved and laterally compressed bases, and have abbreviated cusps. Both the convex and concave edges of the elements are drawn into low keels.

Tortiform elements. (Text-fig. 2O, R) These have been alternatively termed tp by Armstrong (1990; Text-fig. 1). These elements are spatulate, and show torsion of the cusp away from the furrowed



TEXT-FIG. 2. *Panderodus acostatus* (Branson and Branson). Lapworth Museum, University of Birmingham; Kentucky, USA; Brassfield Formation, Silurian, Llandovery; sample collected and donated by R. J. Aldridge, Leicester, UK; ×60. A, D, BU 2258; lateral views of the furrowed and unfurrowed faces of a falciform (pf) element. B, E, BU 2259; lateral views of the unfurrowed and furrowed faces of a high-based asymmetrical graciliform (qg) element. C, F, BU 2260; lateral views of the furrowed and unfurrowed faces of a truncatiform (qt) element. G, J, BU 2261; lateral views of the unfurrowed and furrowed faces of an arcuatiform (qa) element. H, K, BU 2262; lateral views of the furrowed and unfurrowed faces of a low-based symmetrical graciliform (qg) element. I, L, BU 2263; lateral views of an aequaliform (ae) element. M, P, BU 2264; lateral views of the unfurrowed and furrowed faces of a high-based symmetrical graciliform (qg) element. N, Q, BU 2265; lateral views of the unfurrowed and furrowed faces of a low-based asymmetrical graciliform (qg) element. O, R, BU 2266; lateral views of the furrowed and unfurrowed faces of a tortiform (pt) element.

faces. The unfurrowed faces are excavated along their concave margins, while the convex margins are drawn out into sharp edges.

Graciliform elements. (Text-fig. 2B, E, H, K, M, N, P, Q) These have been previously described as asimiliform and similiform (Sweet 1979), ke–pl–tr–oz (Dzik and Drygant 1986), a/b, b, c, (Nowlan and McCracken *in* Nowlan *et al.* 1988), and sym. p (Armstrong 1990; Text-fig. 1). All elements are proclined and generally bicostate. Four morphotypes have been consistently identified in large collections, comprising asymmetric high and low based forms, and sub-symmetrical high and low based forms. In the clusters described below, it has proved impossible to differentiate between these elements, as their lateral faces are largely obscured. Grouping of graciliform elements as a single category is therefore necessary.

Arcuatiform elements. (Text-fig. 2G, J) These are equivalent to the hi of Dzik and Drygant (1986) and the aq of Armstrong (1990; Text-fig. 1). They are generally unicostate elements which show a varying degree of torsion of their erect cusp towards the unfurrowed face. Occasionally, arcuatiform elements have a serrate keel developed on their concave edge.

Truncatiform elements [*new term*]. (Text-fig. 2C, F) These have been recognized as separate morphotypes by Jeppsson (1983*a*, 1983*b*, 1989) who described them as ne elements, and by Armstrong (1990) who described them as r elements (Text-fig. 1). Fåhræus and Hunter (1985) and Dzik and Drygant (1986) illustrated this form as B and sp elements respectively, but felt that they were merely the smallest end-member of the graciliform suite. Truncatiform elements are generally 50 per cent shorter than the graciliforms, and the unfurrowed face is drawn into a slight edge along their convex margin. The cusp is typically elongate, recurved and varies in torsion with respect to the base from species to species.

Aequaliform [*new term*]. (Text-fig. 2I, L) These bifurrowed elements have been illustrated by Sweet (1979, fig. 7.35) as similiform, and by Nowlan and McCracken (*in* Nowlan *et al.* 1988) variously as b/c (pl. 7, figs 23–24) and c (pl. 6, figs 12–13) elements. The only authors to have recognized the unique and consistent occurrence of this element in all *Panderodus* apparatuses have been Jeppsson (1983*a*, 1983*b*, 1989), who referred to this form as tr, and Fåhræus and Hunter (1985) who described these as Group A elements (Text-fig. 1). Dzik (1991) also discussed the presence of bi-furrowed elements, and considered them to be homologous with paired, asymmetrical elements in other apparatuses. These elements are truly symmetrical, and are similar in size to the truncatiform elements.

CLUSTER DESCRIPTIONS

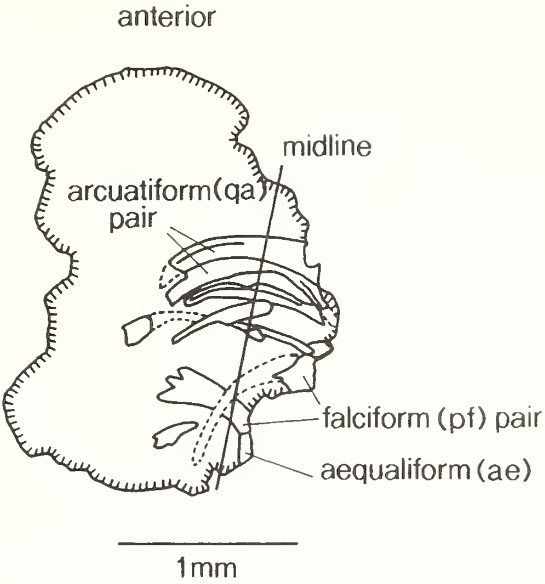
Three clusters and a single bedding plane assemblage are described below in an attempt to elucidate element locations within the *Panderodus* apparatus. As far as possible, the clusters have been selected on the basis of their completeness and structural integrity. Where necessary, sub-clusters within larger specimens have been utilized, but only if they show internal structural consistency *vis-à-vis* consistent element and furrow orientation. The Waukesha bedding plane assemblage provides the necessary architectural framework for the analysis, delineating the anterior and posterior of the apparatus, together with furrow orientation. The remaining clusters serve to fill the gaps in the jigsaw, and thus produce a complete architectural model of the *Panderodus* elemental apparatus.

Waukesha Bedding Plane Assemblage

The single specimen with soft parts preserved (Mikulic *et al.* 1985*a*, 1985*b*; Smith *et al.* 1987), comes from the upper Llandovery Brandon Bridge Konservat Lagerstätte of Waukesha County, Wisconsin, USA, and is the only described coniform euconodont bedding plane assemblage. The presence of a body trace is especially useful as it enables the determination of anterior and posterior in the *Panderodus* apparatus.

The arrangement of elements in the Waukesha bedding plane assemblage (Text-fig. 3) provides constraints for the modelling of three-dimensional apparatus architecture in *Panderodus*, as discussed by Smith *et al.* (1987) and outlined here.

(1) The asymmetrical elements (arcuatiform, graciliform, truncatiform, falciform and tortiform in the terminology used herein) lie in a paired relationship perpendicular to the plane of bilateral symmetry with a posterior and adaxial orientation to the cusp tips.



TEXT-FIG. 3. Camera lucida drawing of the assemblage of elements in the *Panderodus unicostatus* (Branson and Mehl) animal from the Brandon Bridge of Waukesha, Wisconsin, USA, UW4001/7a (part), Geology Museum, University of Wisconsin, Madison; modified from Smith *et al.* (1987, fig. 6.6).

(2) In these elements, the furrowed face shows a consistent orientation, and all the elements on the part have the furrowed faces uppermost.

(3) The arcuatiform element pair lies to the anterior of the assemblage, whilst the falciform element pair lies towards the posterior. An unknown number of pairs of graciliform elements lie between these.

(4) There is no apparent size gradation (*contra* the 'supertooth' model for *Panderodus* presented by Dzik and Drygant (1986)).

(5) The spacing of the elements in the anterior part of the assemblage is closer than that seen at the posterior, which may be either an original feature of the apparatus or the result of flattening of an arched array.

These criteria led Smith *et al.* (1987) to produce an apparatus architecture model for *Panderodus* consisting of two bilaterally opposed, linear and possible arched arrays, which may have been attached to a basal support.

Re-examination of a latex cast of the counterpart and published illustrations of the specimen has enabled the following, additional observations to be made. Firstly, a close study of the overlapping arrangement of the elements shows a consistent stacking with the furrowed faces exposed. Three dimensional modelling of the assemblage has shown that this pattern may only be produced from an opposed linear array by a posterior rotation and collapse of the element cusps with the furrows facing anterior. Secondly, Smith *et al.* (1987) did not recognize the occurrence of the aequaliform element in isolated collections of *Panderodus*, suggesting that such forms were aberrant or extreme morphotypes. However, from studies of discrete collections, it is clear that this element is a consistent and essential component of the apparatus (Jeppsson 1983*a*; Sansom 1992; see also comments by Sweet 1988, p. 57), and must be taken into account in any apparatus reconstruction.

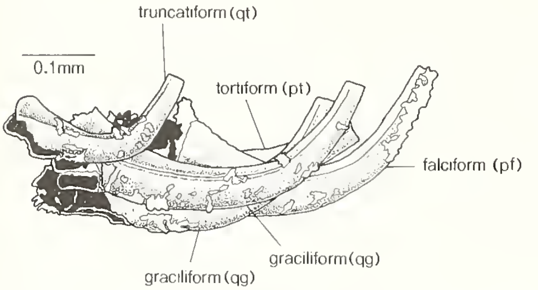
Two small element fragments are found behind the falciform element pair (Text-fig. 3). One of these lies in the same orientation as the paired elements, perpendicular to the plane of symmetry, and would appear to form part of the paired array. The other element is represented by an oblique cross-section, lying parallel to the midline of the assemblage, and the form suggests that this element pointed towards the anterior of the assemblage. Although it may represent the opposing pair of the first element, having been skewed somewhat from its original location, no other pairs show a similar dislocation, as a result this element may be considered as the symmetrical aequaliform element.

Nekézseny Cluster

Described as *Panderodus simplex* (Branson and Mehl) by Kozur (1984) and Balogh and Kozur (1985), this specimen was recovered from a middle Wenlock olistolith within the Devonian Strázsahegy Formation of Nekézseny, northern Hungary.

Panderodus simplex was originally erected as a form taxon and has been synonymized with *Panderodus unicostatus* (Cooper 1976; Armstrong 1990). Although the cluster has been lost (pers. comm. Kozur 1990), the illustrated elements show a number of differences from *Panderodus unicostatus*, notably that they are more recurved and robust. Until additional material is available for study, this specimen is best assigned to *Panderodus* aff. *P. unicostatus* (Branson and Mehl).

Five elements are joined along their lateral faces and they all have the same furrow orientation. Little post-mortem deformation is apparent, although the base of the falciform element is slightly displaced from the bases of the other elements. Text-figure 4 shows the cluster viewed anteriorly, and identifies the element order. Based upon the furrow orientation seen in the Waukesha bedding plane assemblage, the element order from anterior to posterior in this cluster is truncatiform, graciliform, graciliform, falciform and tortiform. The Nekézseny cluster represents a complete posterior portion of half of a *Panderodus* apparatus.



TEXT-FIG. 4. Cluster of *Panderodus* aff. *P. unicostatus* (Branson and Mehl) elements from a middle Wenlock olistolith within the Devonian Strázsahegy Formation, Nekézseny, northern Hungary. Illustrated by Kozur (1984, pl. 1 fig. 1) and Balogh and Kozur (1985, pl. 1 fig. 1) as *Panderodus simplex* (Branson and Mehl), this specimen has subsequently been lost (Kozur, pers. comm. 1990).

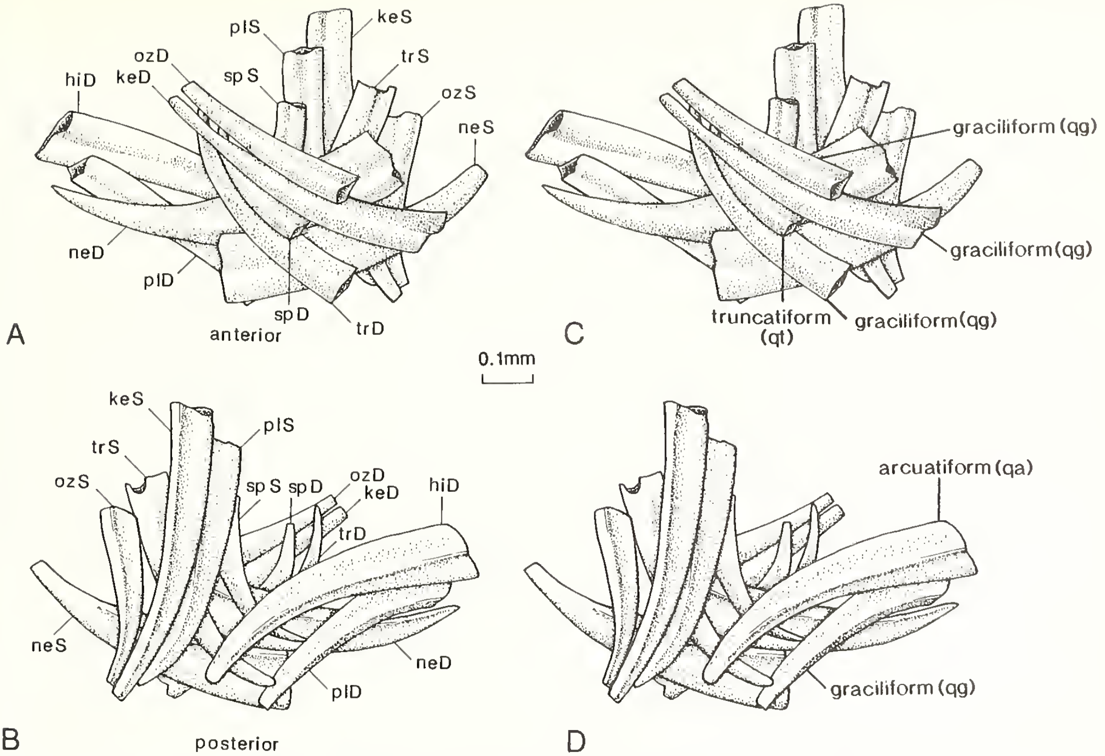
Podolia Cluster

This cluster (Text-fig. 5), consisting of thirteen elements identified as *Panderodus unicostatus* by Dzik and Drygant (1986), is from the Llandovery Teremcy Beds of Podolia, Ukraine. The specimen appears to have undergone considerable taphonomic deformation from the original element arrangement; however, all the elements appear to be asymmetrical and paired. Dzik and Drygant (1986) proposed a three-dimensional model for this cluster based on a size gradation through the elements. This gradation is more conceptual than observable, and the grasping apparatus of protoconodonts and chaetognaths seem to have acted as a template for their reconstruction. In order to explain the preservation of the Podolia cluster, it was necessary for Dzik and Drygant (1986, fig. 2B) to invoke a complex series of apparently random dislocations.

Whilst the cluster has been considerably deformed, two relatively coherent subclusters can be recognized and are of use in architectural restoration. These sub-clusters are selected on the basis of their lateral superposition and spatial arrangement. The similarity in cusp/furrow orientation shows them to have been derived from the same half of the apparatus.

Sub-cluster 1 (Text-fig. 5A, C) consists of four elements. The visible lateral faces of these elements are unfurrowed. The element order is a single graciliform, truncatiform, and two graciliforms. Correlation with the Nekézseny cluster is provided by the presence of two, elongate graciliform elements lying to the posterior of a short, recurved truncatiform element, and from the evidence of the Podolia cluster, an additional graciliform element lies to the anterior of this element.

The smaller sub-cluster 2 (Text-fig. 5B, D) lies on the opposite side of the main cluster, and consists of two elements. Both of the exposed faces are furrowed, the anteriormost is of arcuatiform



TEXT-FIG. 5. Cluster of *Panderodus unicostatus* (Branson and Mehl) elements from the Teremcy Beds, upper Llandovery, Studencyia, Podolia, Ukraine; ZPAL C.XV/2, Zaklad Paleobiologii PAN, Warszawa, Poland. A, B, redrawn from Dzik and Drygant (1986, fig. 3) following their notation; C, sub-cluster 1 of four elements; D, sub-cluster 2 consists of two elements.

morphology, and the element behind is a graciliform. The presence of the arcuatiform element to the anterior of the apparatus is also evident from the Waukesha assemblage.

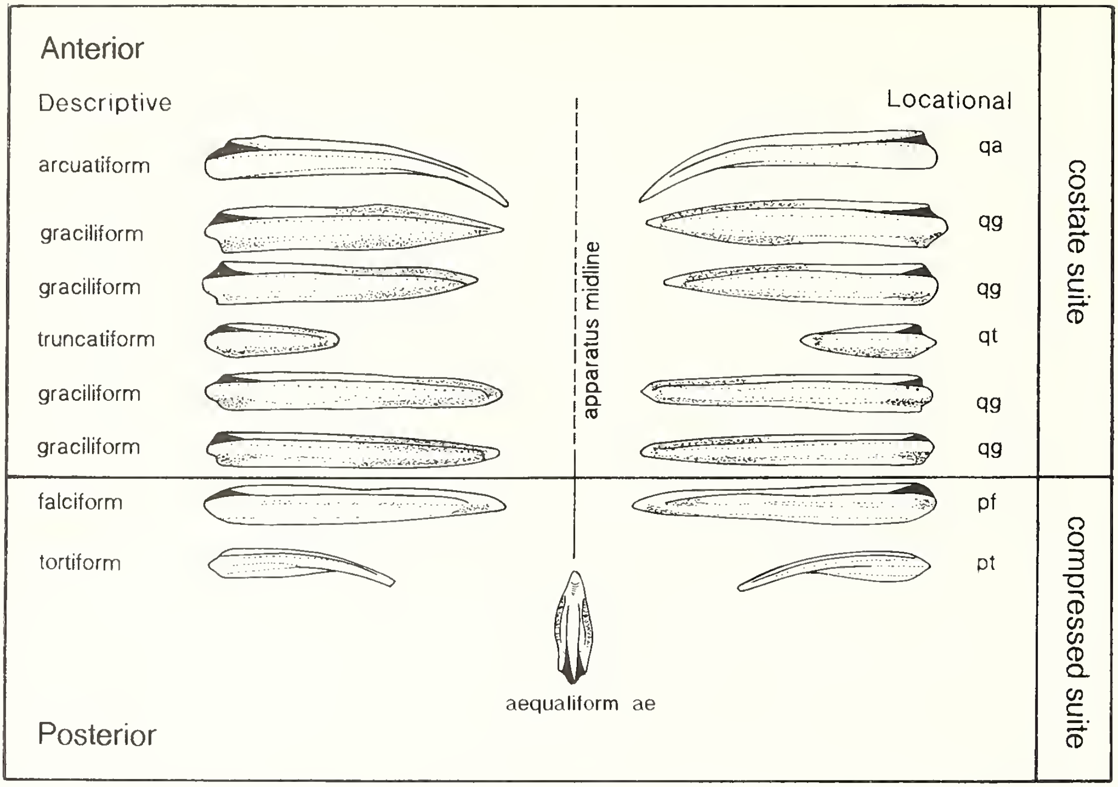
Shandong Cluster

Additional evidence is provided by a three element cluster (An *et al.* 1983; pl. 32, fig. 17*a–c*) from the Shandong Province of North China. This consists of a pair of graciliform elements lying adjacent to a single falciform element.

CLUSTER CORRELATION

Dzik and Drygant (1986) and Smith *et al.* (1987) concluded that the apparatus consisted of fourteen elements, whilst Jeppsson (1983*a*) implied a figure closer to 100. The latter figure was derived from the relative abundance of the symmetrical aequaliform element (tr of Jeppsson 1983*a*) in his discrete collections. Under-representation of this element could be due to its relatively small size and the possibility of selective hydrodynamic sorting in the environment of deposition (McGoff 1991), and/or loss through the sieve during processing (Jeppsson 1983*a*).

The identification and correlation of repeated element sequences in the clusters outlined above, permits formulation of the complete *Panderodus* apparatus (Text-fig. 6). The apparatus consists of seventeen elements, sixteen of which are found in two bilaterally opposed linear arrays. This element number is the same as that which may be inferred from discrete collections, suggesting that each



TEXT-FIG. 6. Architectural reconstruction of the *Panderodus* apparatus showing the differentiation of the paired elements into an anterior costate suite and a posterior compressed suite. The aequaliform ae element is thought to have lain on the midline somewhat to the posterior of the apparatus.

morphotype (including the four sub-divisions within the graciliform category) is a consistent component of the apparatus.

The apparatus plan of *Panderodus* falls into two suites of paired elements, an anterior costate suite and a posterior acostate, compressed suite (Text-fig. 6). The costate suite consists of an anterior pair of twisted unicostate arcuatiform elements, behind which are found four pairs of graciliform elements divided into two units by the truncatiform pair. The posterior compressed suite consists of the falciform and tortiform pairs. The final component of the apparatus is represented by the single aequaliform element lying along the apparatus midline. The medial placement of the aequaliform element is contrary to the interpretation of Dzik (1991) who argued that these elements occurred in pairs orientated perpendicularly across the plane of bilateral symmetry. This is the only truly symmetrical element in the apparatus, supporting a location on the midline.

The integrity of the genus Panderodus

Nowlan and Barnes (1981) and Nowlan and McCracken (*in* Nowlan *et al.* 1988) have suggested that a variety of apparatus styles are present within the genus *Panderodus*, and they questioned the generic assignment of those species which did not follow the *Panderodus unicostatus* apparatus plan. However, the available evidence from cluster data and discrete collections of well known species refutes the presence of more than one apparatus plan within the genus.

In those species of *Panderodus* which are well understood and for which large collections are available, it is possible to homologize all of the elements of the apparatus on morphological criteria

(Text-fig. 7) and identify the presence of a costate suite (arcuatiform and graciliform-truncatiform) and a compressed suite (falciform-tortiform) of paired elements. The symmetrical aequaliform is also consistently present. *Panderodus* is a unified genus based upon a single apparatus architecture, comprising three locational domains. Species can be diagnosed by variations in element morphology.

HOMOLOGY BETWEEN CONIFORM CONODONT APPARATUSES

Coniform locational nomenclature

Having established an architectural model for *Panderodus* it is now possible to propose a locational notation. The modified version of Sweet's (1979) nomenclature employed above is not applicable, since it is purely descriptive rather than locational; the aim here is to demonstrate locational homology, not a morphological comparison of elements. The locational scheme utilized here is an adaptation of the notation of Barnes *et al.* (1979), and subsequently modified by Armstrong (1990). It is important to emphasize that this scheme is now redefined in a locational sense and reference to its previous usage should be made with care.

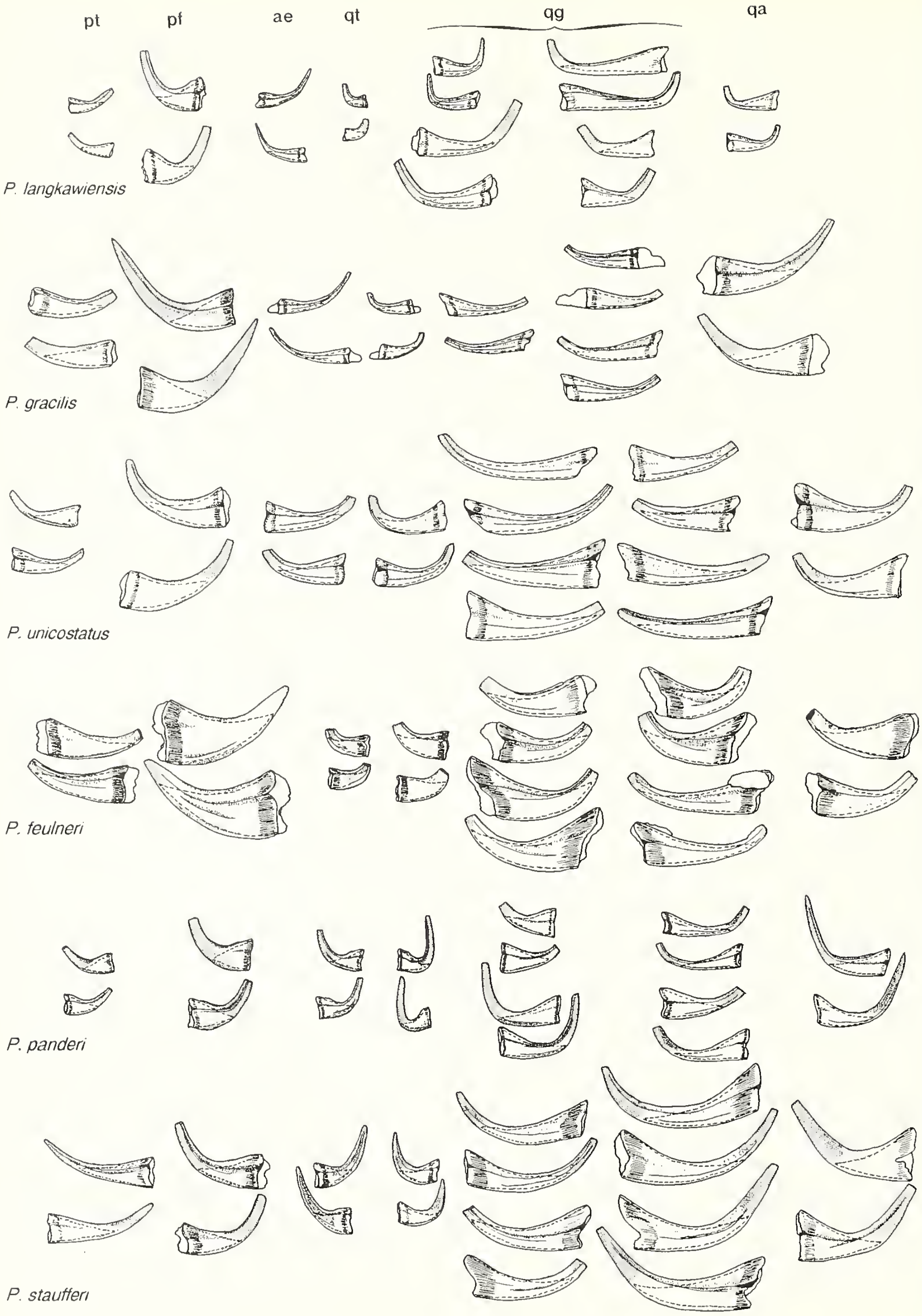
Armstrong (1990) refined the notation of Barnes *et al.* (1979) as a binomial scheme, one letter referring to general element shape and the other to cross-sectional shape and symmetry. As the location of the elements in *Panderodus* has been established, it is possible to further modify this scheme so that it reflects element position. The differentiation of the paired assemblage into two components is recognized by terming the anterior suite as 'q elements' and the posterior suite as 'p elements'. Further subdivisions of the element positions are denoted by a second letter (Text-fig. 6).

This notation, although developed from the element categories in *Panderodus*, has the advantage of being locational, and it is possible to compare coniform architectures where suitable data are available. The identification of homologous elements should lead to a 'natural' suprageneric classification, as suggested by Armstrong (1990), on the basis of apparatus similarities and/or reduction of elements in evolutionary lineages. A number of genera have been studied in an attempt to determine the wider applicability of the *Panderodus* apparatus model, although only genera known from clusters and closely related forms are discussed. Many coniform apparatuses are, as yet, incompletely understood. It is important to establish whether incompleteness of apparatus reconstruction is a result of biological, taphonomic or collection processes, as these characters are used to differentiate between apparatuses at the suprageneric level.

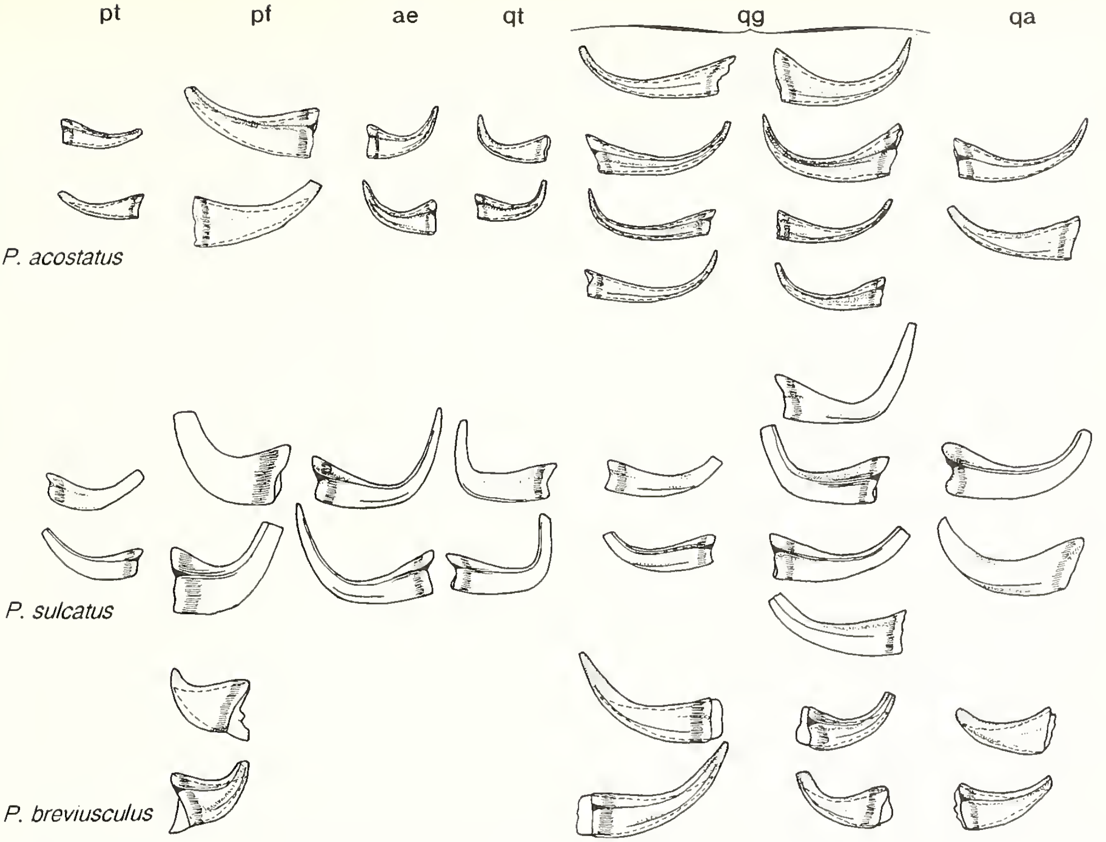
Applicability of the Panderodus *apparatus model to other panderodontid lineages*

Belodina compressa (*Branson and Mehl*). This species has been reconstructed by Nowlan (1979) and Sweet (1979) as a trimembrate apparatus consisting of elongate, slender, denticulate grandiform elements; tightly recurved, broad denticulate compressiform elements; and geniculate adenticulate eobelodiniform elements.

Barnes (1967) and Nowlan (1979) figured three clusters, and using these it is possible to develop an architectural model for *Belodina compressa*. For purposes of orientation, it is assumed that the position and function of lateral furrows in *Belodina* is homologous with *Panderodus*; this is substantiated by the similarity in structure and histology of the two genera (Barnes, Sass and Poplawski 1973). The cluster illustrated by Barnes (1967, text-fig. 2) and refigured by Nowlan (1979, fig. 35.2), shows minor dislocation in the position of the four component elements, but provides evidence for architectural homology with *Panderodus*. Within this four element cluster, three elements were described as grandiform and have the same furrow orientation, suggesting that they represent an undeformed sub-cluster. The anteriormost grandiform element is approximately half the size of the other elements and constitutes a new element not previously described from discrete element collections. The furrowed face of the remaining compressiform element lies in the opposite direction to the others, an orientation probably resulting from post-mortem dislocation. The remaining clusters figured by Nowlan (1979, pl. 35.1, figs 1–5 and pl. 35.1, figs 6–10) are both



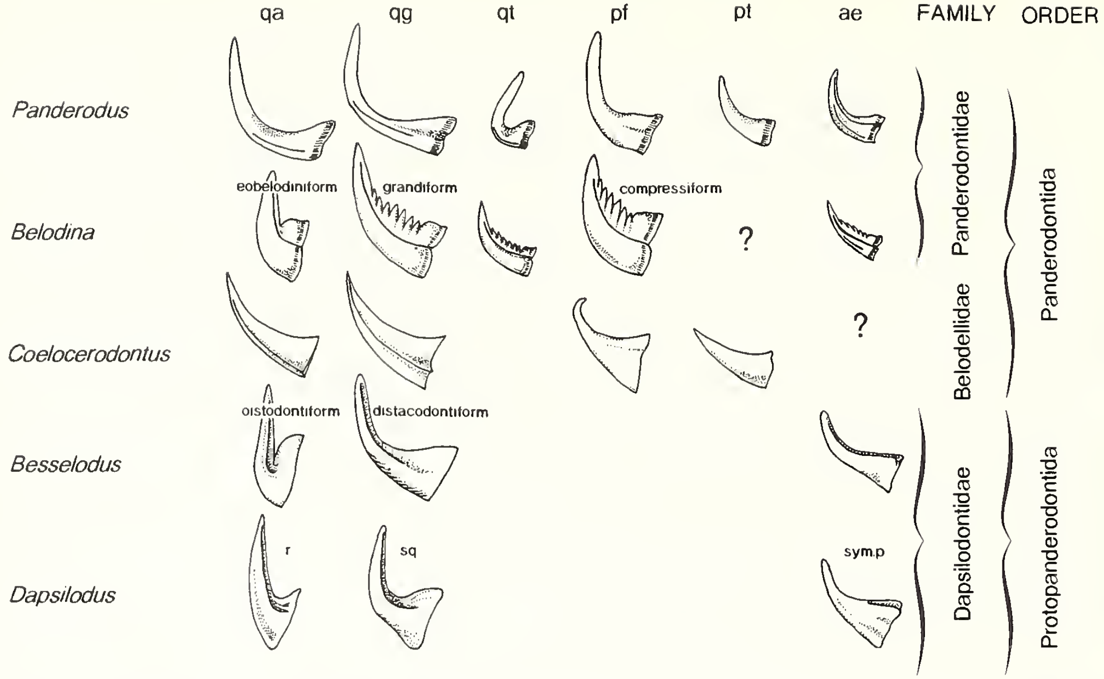
TEXT-FIG. 7. For legend see opposite.



TEXT-FIG. 7. Elements and apparatuses of nine species of *Panderodus*, showing the development of the basal cavity (dashed line) and distribution of white matter (shaded); not drawn to scale. Illustrated apparatuses are based upon elements figured by Sansom (1992), and a revision of the taxonomy of *Panderodus* is currently underway. The internal details of *P. sulcatus* are not known, and the *P. breviusculus* apparatus has not yet been fully reconstructed. *P. langkawiensis* (Igo and Koike); Gotland, Sweden; Lower Visby Beds, Silurian, Llandovery. *P. gracilis* (Branson and Mehl); Washington Land, North Greenland; Lafayette Bugt Formation, Silurian, Llandovery. *P. unicostatus* (Branson and Mehl); Missouri, USA; Bainbridge Formation, Silurian, Ludlow. *P. feulneri* (Glenister); Wulff Land, North Greenland; Morris Bugt Group, Ordovician, Caradoc. *P. panderi* (Stauffer); Leijiatun, China; Xiushan Formation, Silurian, Llandovery. *P. staufferi* (Branson, Mehl and Branson); Gotland, Sweden; Upper Visby Beds, Silurian, Wenlock. *P. acostatus* (Branson and Branson); Kentucky, USA; Brassfield Formation, Silurian, Llandovery. *P. sulcatus* (Fåhræus); Jämtland, Sweden; Flåsjö Formation, Ordovician, Llanvirn. *P. breviusculus* Barnes; Wulff Land, North Greenland; Morris Bugt Group, Ordovician, Caradoc.

formed from two elements, and consist of a grandiform element in juxtaposition with an eobelodiniform element and a broken compressiform or grandiform element respectively. In the former case the furrows are opposed whilst in the latter they face in the same direction.

It is probable that the grandiform elements of *Belodina* and the graciliform elements of *Panderodus* are homologous (Text-fig. 8) and they both occupied the qg positions. In both genera these elements are elongate and slender, and occurred as multiple pairs. The *Belodina* compressiform element is morphologically similar to the falciform element occupying the pf location in *Panderodus*. The small, truncated grandiform element of *Belodina* compares with the truncatiform (qt) element of *Panderodus* in being considerably shorter than the elements occupying the qg locations. The erect cusp of the eobelodiniform element of *Belodina* shows a degree of torsion away from its furrowed lateral face, a feature seen in the arcuatiform elements occupying the qa position in *Panderodus*.



TEXT-FIG. 8. Apparatus homologies and putative suprageneric reclassification of the coniform taxa discussed in the text; not drawn to scale. Descriptive terminology for *Belodina* is from Nowlan (1979), for *Besselodus* from Aldridge (1982) and *Dapsilodus* from Armstrong (1990). The presence of additional elements in *Belodina*, *Coelocerodontus* and *Besselodus* is discussed in the text.

Clusters and published reconstructions of *Belodina compressa* lack tortiform (pt) and aequaliform (ae) homologues. Nowlan and Barnes (1981) included torted, spatulate elements, morphologically similar to the pt, in the grandiform suite of *Belodina arca* Sweet and *Belodina dispansa* (Glenister). In addition, small, double furrowed belodinid elements have been included in Gen. *et*. sp. nov. A of McCracken (1987, pl. 1 figs 16, 21, 22). These occur in samples containing *Belodina confluens* Sweet and it is possible that these elements may be part of a single apparatus. If this is the case, the double furrowed elements would be ae homologues and the apparatus of *Belodina* would comprise the three locational domains identified in *Panderodus*. This new concept is consistent with the familial classifications of Clark (1981), Sweet (1988) and Dzik (1991).

Wider applicability of the Panderodus *apparatus model*

Clusters of coniform elements have also been described for *Coelocerodontus*, a member of the Family Belodellidae (*sensu* Sweet 1988), and *Besselodus* (Family Unknown *sensu* Clark 1981; Family Daposilodontidae *sensu* Sweet 1988; Family Strachanognathidae *sensu* Dzik 1991).

Coelocerodontus *Ethington*. Andres (1988) illustrated clusters of *Coelocerodontus*, from the Tremadoc of Öland, and proposed an apparatus architecture (Andres 1988, fig. 17) which comprised an anterior, unicostate element (equivalent to the qa element in the *Panderodus* apparatus), a suite of at least five, bicostate (qg) elements, a laterally compressed (pf) element and a torted, unicostate (pt) element at the posterior of the paired assemblage. A qt element is not seen in the clusters or has been described as a discrete element. Given the apparent completeness of these clusters, it seems likely that this position was occupied by an element with a similar morphology to those occupying the qg locations in the *Coelocerodontus* apparatus.

Müller and Hinz (1991, pl. 41, figs 11, 14, 16) illustrated two well-preserved clusters of *Coelocerodontus*. In one of these (pl. 41, figs 11, 14), a short element is present. This was not included in their apparatus reconstruction, and has not been previously described from discrete elements collections. The size and shape of this element suggests it may be an ae homologue. If this is the case, then *Coelocerodontus* has elements in the three locational domains described for the Panderodontida (Text-fig. 8).

Besselodus *Aldridge and* Dapsilodus *Cooper*. These two genera are considered to be closely related (Sweet 1988) and are considered together. Aldridge (1982, pl. 44, figs 1–4) described a cluster of *Besselodus* from the Aleqatsiaq Fjord Formation of Washington Land, western North Greenland. This comprises six distacodontiform (qg) element and a single oistodontiform (qa) element. An additional, symmetrical (ae) element was reported by Nowlan and McCracken (*in* Nowlan *et al.* 1988, pl. 2, figs 7–8, 13–15).

Dapsilodus was described as trimembrate by Cooper (1976) and Armstrong (1990). Armstrong separated sym. p elements (ae), sq elements (qg) and r elements (qa). The ae element occurred with a relatively low abundance of one to fifteen qg and qa elements. The apparatus structures of *Dapsilodus* and *Besselodus* are identical and are divisible into a qa pair, a costate qg suite and a single ae element. They differ from *Panderodus* as both *Dapsilodus* and *Besselodus* lack a distinct posterior suite of p elements (Text-fig. 8).

Implications for coniform suprageneric classification

Recent high level classifications (Sweet 1988; Dzik 1991; Aldridge and Smith 1993) have focussed on apparatus structure and morphological homology between elements, but must be considered probationary pending further information (Armstrong 1990; Aldridge and Smith 1993). Although we have only discussed apparatus homology in five coniform genera, it is clear that architectural homology provides one of the few testable ways by which a biologically sound suprageneric classification for conodonts can be established.

The identification of shared apparatus components leads to a re-definition of the Family Panderodontidae, and it is proposed here that all coniform apparatuses whose elements possess a panderodontid furrow and are thought to exhibit a fully developed apparatus (see Text-fig. 8) should be placed within this suprageneric unit. *Panderodus* and, with less certainty, *Belodina* belong here. Other genera which have previously been included within the panderodontids include *Pseudoobelodina*, *Parabelodina*, *Culumbodina* and *Plegagnathus* are known from small collections from the middle and upper Ordovician, and have been reconstructed as quadrimembrate or quinquemembrate apparatuses (Sweet 1988). Given the low abundance of elements referable to these forms, their classification within the Family Panderodontidae is based only upon their development of a panderodontid furrow, and perhaps this should be questioned until further information on their apparatus structure is forthcoming.

It is also proposed that all coniform apparatuses which exhibit differentiation into an anterior qa–qg domain, a posterior pf–pt domain, and a symmetrical ae component should be reclassified within the Order Panderodontida. The presence of a truncated qt element may be a feature of the Panderodontidae, but in other apparatuses it does not appear to be differentiated. Both Sweet (1988) and Aldridge and Smith (1993) rejected any phylogenetic relationship between *Coelocerodontus* and *Panderodus*, placing the former in the Order Belodellida and the latter in the Order Panderodontida. The similarity between the apparatus model of Andres (1988) for *Coelocerodontus*, together with the possible presence of an additional ae component (see discussion above), and the apparatus of *Panderodus* suggests that they should be united within the Order Panderodontida. In addition, Jeppsson (1989) has proposed morphological homology between the apparatuses of *Belodella* and *Panderodus* based upon large discrete element collections. If this observation can be further substantiated with architectural data, then the Family Belodellidae should be transferred to the Order Panderodontida (Dzik 1991).

Besselodus and *Dapsilodus* were classified within the Order Belodellida by Sweet (1988), which was combined with the Order Panderodontida by Dzik (1991), whilst Aldridge and Smith (1993) placed the two genera in their Order Protopanderodontida. The homology proposed here between these two apparatuses and that of *Panderodus* (Text-fig. 8) suggests that *Besselodus* and *Dapsilodus* lack a posterior domain of p elements. This feature of their apparatuses places them outside of the concept of the Order Panderodontida adopted here. McCracken (1989) has reconstructed the apparatus of *Protopanderodus* with a morphological transition series of costate a/b-c elements (?qg homologues) and grooved e elements (morphologically similar to the qa elements of *Besselodus* and *Dapsilodus*). This similarity in apparatus structure argues in favour of following Aldridge and Smith (1993) in including *Besselodus* and *Dapsilodus* within the Order Protopanderodontida.

POSSIBLE HOMOLOGY WITH RAMIFORM-PECTINIFORM APPARATUSES

If conodonts form a monophyletic clade (Conway-Morris 1989), then it is a logical step to try and develop a unified locational apparatus notation, which would allow direct homology to be drawn between ramiform-pectiniform and coniform apparatuses. Many authors have proposed universally applicable schemes (Barrick 1977; Orchard 1980; Sweet 1988; Nowlan and McCracken *in* Nowlan *et al.* 1988) based purely on morphological comparisons of elements, whilst others have used locational models for coniform apparatuses which we consider erroneous (Dzik and Drygant 1986; Dzik 1986, 1991). The proposed unification of a coniform apparatus notation enables comparison with ramiform-pectiniform apparatuses.

Both types of apparatus show a similar broad differentiation into three locational domains. In the ramiform-pectiniform system based upon ozarkodinid architecture, apparatuses can be described as comprising an anterior, symmetry transition series of S elements (including a symmetrical Sa), lateral M elements and posteror P elements. Sb, Sc, Sd and M, and P elements fall into two morphologically, locationally and functionally distinct units. The Sa element is assumed to lie on the midline of the apparatus and is associated with the S and M elements (Aldridge *et al.* 1987). In our locational scheme for coniforms the fully developed apparatus, typified by *Panderodus*, contains the qa–qg–qt–qg domain, the pf–pt domain and the ae element.

Although such a comparison appears to be compelling, it overlooks a potentially crucial difference between the two architectures. The orientation of the anterior paired elements with respect to the apparatus midline is diametrically opposed. In coniform apparatuses they lie perpendicular to the plane of symmetry, and in ramiform-pectiniforms they are parallel (Smith 1990). At present, no intermediates between these architectural types are known. Without relevant architectural information from Lower Ordovician taxa, it is possible that broad agreement in apparatus style may reflect functional convergence rather than actual locational homology. If architectural information is forthcoming for primitive conodonts, it may be possible to derive a universally applicable nomenclatural scheme based upon such a model. Current restriction of our knowledge to two widely divergent clades argues in favour of a conservative approach to apparatus homology.

CONCLUSIONS

Detailed analysis of published clusters and knowledge of element morphologies from large dicrete collections has enabled the development of an apparatus architecture model for *Panderodus*. This enables a redefinition of the species concept for this genus, with the apparatus consisting of eight element pairs and a single symmetrical component. Architecturally, the *Panderodus* apparatus is divisible into three locational domains, the anterior qa–qg–qt–qg paired costate suite, the posterior pf–pt compressed elements, and the symmetrical component which lies along the apparatus midline.

The comparison of other coniform taxa with the *Panderodus* apparatus has initiated a reassessment of their suprageneric classification. It is proposed that those coniform apparatuses, which exhibit a general differentiation into the same three locational domains identified in *Panderodus*, are placed within the Order Panderodontida. Apparatuses which follow the *Panderodus* plan precisely, including qt elements, and also possessing panderodontid furrows, are included within the Family Panderodontidae. The identification of homologous apparatus components is aided by the development of unified locational notation specific to coniform conodonts.

Although there are now two well-founded architectural models for conodont apparatuses, these are based upon the morphologically distinct and separate panderodontid and ozarkodinid lineages. This degree of phylogenetic separation and differences in the orientation of the apparatus components with respect to the apparatus midline hampers the recognition of homologous element locations, thus the development of a unified notational scheme is deferred until further data is available. Only with additional architectural data will it be possible to establish a stable suprageneric classification for all conodonts, and hence propose macroevolutionary models for the development of the oral apparatus of the earliest vertebrates.

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NEW TRIASSIC ISOPOD CRUSTACEANS FROM NORTHERN ITALY

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ABSTRACT. Two new Triassic isopod crustaceans from the southern Calcareous Alps are described on the basis of well preserved specimens. This small assemblage comes from the late Norian Calcare di Zorzino, which is especially well-known for its vertebrate fauna. At least two new genera of Isopoda are present, here assigned to the Sphaeromatidae and Serolidae. *Triassphaeroma magnificum* is erected for specimens whose single first pleonal unit comprises five fused tergites, a feature peculiar to Sphaeromatidae. *Elioserolis alpina* is the first definitive fossil representative of the Serolidae so far known; attribution is on the basis of the round shape, head inserted in the first pereionite, and reduced number of pleionites. Specimens are preserved in a way which indicates that the biphasic moulting of Recent isopods had already evolved in late Triassic serolids.

THE Calcare di Zorzino (Zorzino Limestone) of Lombardy, northern Italy, was deposited in an anoxic environment (Tintori 1992), and it has yielded an abundant, well-preserved fauna. Although fishes (about forty genera) and reptiles (more than ten genera) make up its bulk, invertebrates are also well represented. Crustaceans were among the first elements to be studied (Pinna 1974), but subsequent research has focused mainly on vertebrates (Wild 1978; Tintori 1983, 1992; Renesto 1994). Fieldwork and preparation of material are still in progress. Interesting new specimens, belonging to poorly known groups, are commonly discovered, such as the isopod crustaceans which are the subject of this paper. The good, sometimes three-dimensional preservation of several specimens has allowed a complete restoration of the dorsal exoskeleton of the sphaeromatid *Triassphaeroma magnificum* gen. et sp. nov.; and two flattened specimens are ascribed to the serolid *Elioserolis alpina* gen. et sp. nov. The Calcare di Zorzino yielded a further isopod taxon, represented by a single, poorly preserved specimen, which is not described here. It is rather long (somewhat less than 20 mm), with everted head, seven large pereionites and six small free pleonites. Uropod insertion is not visible, so we cannot give a confident attribution, but it seems to be closely comparable to oniscoidean isopods. All the specimens of *Triassphaeroma magnificum* are from a locality at Endenna, and the other specimens are from a nearby locality designated 'Zogno 2'.

GEOLOGICAL SETTING, PALAEOENVIRONMENT AND TAPHONOMY

The Calcare di Zorzino is considered to be of middle–late Norian (Late Triassic) age, mainly on the basis of its stratigraphical position. It is coeval with the topmost part of the Dolomia Principale, a carbonate platform extending from Spain to Greece (Jadoul *et al.* 1992). The fossiliferous beds lie in the uppermost part of the Calcare di Zorzino and, based on evidence from the evolution of *Saurichthys* (Tintori 1990), they are dated around the boundary between the Alaunian and Sevatian (middle–late Norian).

The Calcare di Zorzino was deposited in basins which were probably a few hundred metres deep in their centres, where they were anoxic (Jadoul 1986; Jadoul *et al.* 1992), and had shallow margins of variable width, where the water was oxygenated (Tintori in press). An invertebrate fauna thrived along these margins, dominated by bivalve molluscs (mainly *Modiolus* and *Isognomon*) and crustaceans (Pinna 1974). Gastropods, echinoderms, brachiopods and corals were also present, but are rarely represented in the fauna. In order to be fossilized, the remains of all these organisms had

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to be transported to the anoxic portion of the basins; otherwise, they would have been destroyed by the dolomitization that affected the shallow-water sediments in the area where they are inferred to have lived. From the shelled invertebrates, as well as from the durophagous vertebrates that fed on them (Tintori in press), we can infer that the oxygenated margins of the basins, up to a depth of 20–30 m, supported the richest benthic community. But since all of the fossils are found in the anoxic sediments, they must be considered as allocthonous.

Two main benthic environments can be distinguished: a rim of small patch reefs and organic mounds that bordered the basins (Jadoul *et al.* 1992) and, towards the basin centre, a muddy-bottomed area, colonized by the bivalve fauna. Specialized durophagous and semidurophagous fishes (Tintori in press) probably fed on the bivalves, picking them up with their anterior chisel-shaped or elongated teeth and crushing the shells with their stout, inner dentition.

Hard and soft substrates were both available to small organisms such as isopods. Living sphaeromatid isopods are widespread in brackish to marine waters, down to a few metres depth. They are usually associated with sea-weeds, barnacles or mussel beds, which provide shelter against wave and current action (Naylor 1972). For further protection, sphaeromatids are usually capable of enrollment. Living in rough surfaced environments, their dorsal exoskeleton is often well ornamented (Dumay 1971). Thus, the environments occupied by sphaeromatids today are very similar to those inferred to be present along the margins of the Norian basin, especially the shallow-water mussel beds.

By analogy with living species, the functional morphology and poor mineralization of the exoskeleton of the fossil Serolidae suggest a soft-bottomed, low energy habitat. Thus, *Elioserolis* probably inhabited a deeper and quieter area than the mussel community.

The Norian fauna is usually very well preserved; almost all vertebrate and arthropod specimens are complete and fully articulated (Tintori 1992). Only in a few cases are distal parts missing, owing to post-mortem transport.

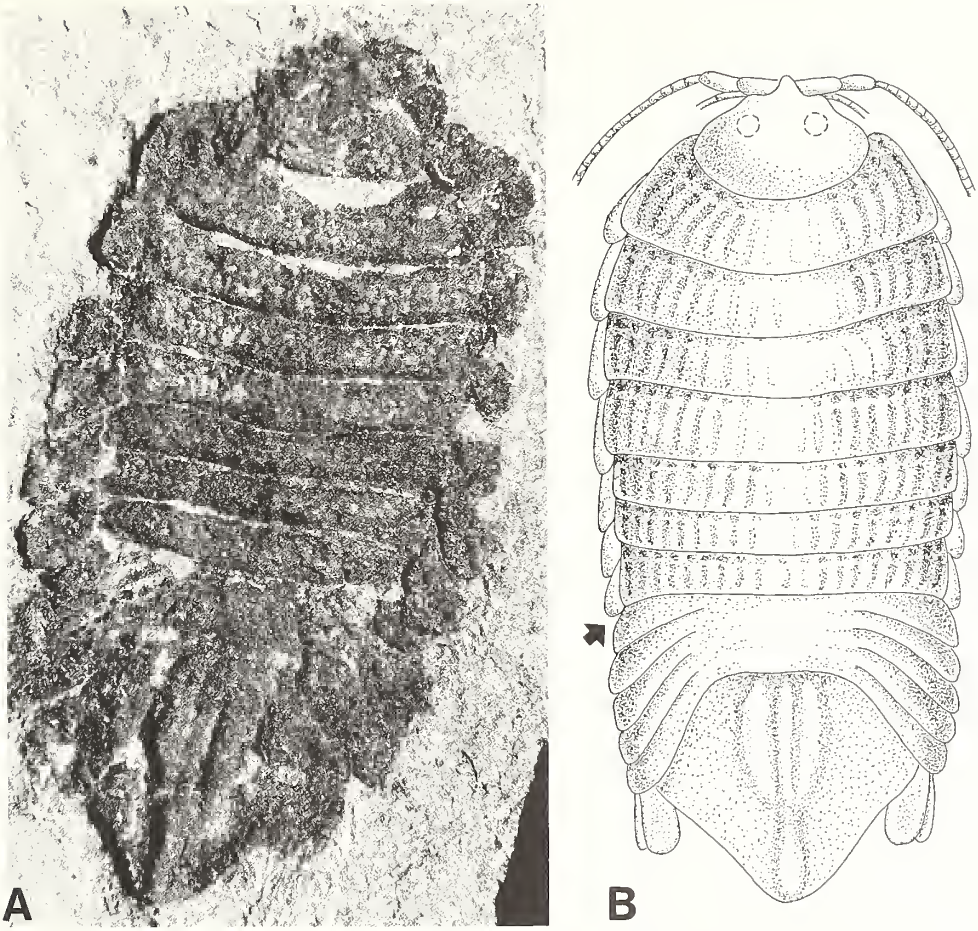
Because the sphaeromatids are complete, at least in the dorsal exoskeleton, they may have reached the anoxic area whilst still alive. Alternatively, since appendages are not visible in most of our specimens, they might be exuviae. In this case, these may have sunk into the anoxic waters after transport over a short distance by very weak currents. Biphasic moulting, which is typical of many isopods (George 1972), is evident in *Elioserolis*, as shown by the peculiar aspect of both specimens. Both show a much more mineralized anterior (head plus the four anterior pereionites) than posterior region (the three posteriormost pereionites and the pleonites). Since head and appendages are all present, specimens are thought to be dead individuals rather than exuviae. Thus, they possibly died during moulting, just after shedding the old dorso-posterior region of the exoskeleton. *Triassphaeroma* does not show any evidence of biphasic moulting.

On some specimens the original microstructure of the exoskeleton of *Triassphaeroma* is well preserved. Both micro- and macro-ornamentation are shown (Text-fig. 2A–C). In a few specimens, the inner side of the dorsal exoskeleton is visible, but shows little detail. Specimens preserved in marly limestone are very thin, but show impressions of appendages. *Elioserolis* and the undetermined specimen from locality 'Zogno 2' are also preserved as thin, organic films on the lamina surface.

SYSTEMATIC PALAEONTOLOGY

Class MALACOSTRACA Latreille, 1806
Superorder PERACARIDA Calman, 1904
Order ISOPODA Latreille, 1817
Suborder FLABELLIFERA Sars, 1882
Family SPHAEROMATIDAE H. Milne-Edwards, 1840 [*nom. correct.* Dahl, 1916]
Genus TRIASSPHAEROMA gen. nov.

Derivation of name. From the age of the fossil material combined with the name of the living genus.



TEXT-FIG. 1. *Triassphaeroma magnificum* gen. et sp. nov. A, MPUM 6692, holotype; Calcare di Zorzino (Triassic, Norian); Endenna, Zogno, Bergamo, northern Italy; note the antennae bases, the macro-ornamentation, the first pleonal unit showing traces of segmentation and longitudinal ridges on the pleotelson; × 15. B, restoration in dorsal view; the arrow points to the boundary between the pereion and the pleon.

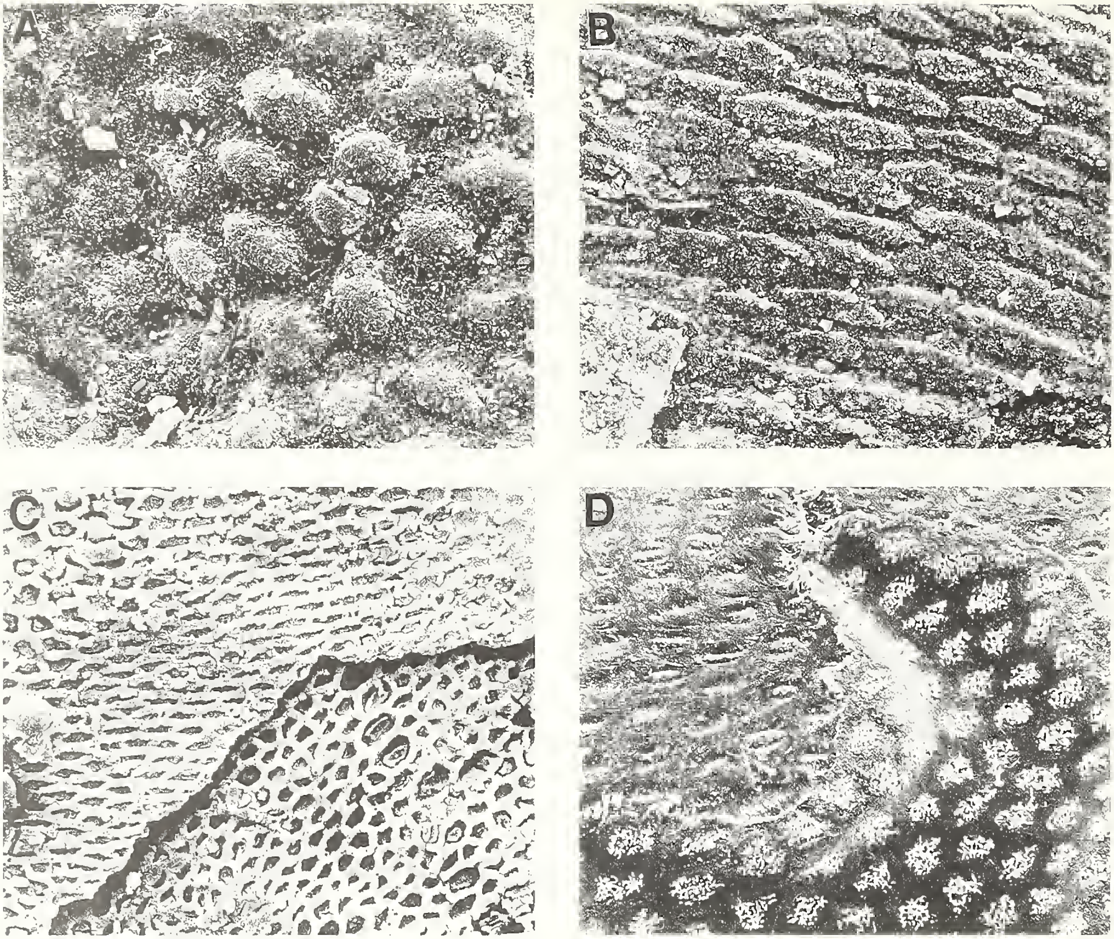
Diagnosis. Body ovoid, about three times as long as wide (pereionite width); cephalon as long as the first pereionite, in which it is partially sunken, but narrower (width about 65 per cent of the first pereionite); pereionites ornamented with pits and longitudinal furrows; epimeres well defined, transversely elongated, rhomboidal; anterior unit of pleon made up of five fused pleonites with suture lines only on the lateral regions; subtriangular telson rather pointed with median and lateral longitudinal ridges, each bearing a large tubercle; biramous, smooth-edged uropods about two-thirds the length of the telson; pereionites ambulatory.

Triassphaeroma magnificum sp. nov.

Text-figures 1, 2A–C

Derivation of name. Latin, *magnificum*, reflecting the fine preservation of most specimens.

Types. The holotype MPUM 6692 (Palaeontological Museum of the Università degli Studi di Milano) and seventeen paratypes (MPUM 6693–6707 and MPUM 7034–35). Three specimens have counterparts.



TEXT-FIG. 2. A–C, *Triassphaeroma magnificum* gen. et sp. nov. Calcare di Zorzino; Endenna, Zogno, Bergamo, northern Italy; A, details of micro-ornamentation in the anterior region of a pereionite; MPUM 6706; × 1700; B, details of micro-ornamentation in the posterior region of a pereionite; MPUM 6706; × 1100; C, details of cuticular microstructure; note the double reticulate sheets; MPUM 6707; × 500; D, *Cymodoce* sp. Pontian Archipelago, western Mediterranean, at 69 m depth; details of cuticular microstructure; cavities in the reticular pattern are occupied by chromatophores; × 750. All scanning electron micrographs.

Preservation depends on the lithology: in dark grey limestone the shape of the body and the morphology of the somites as well as their ornamentation are clearly evident. The specimens found in light brown marls show traces of the appendages. All from Calcare di Zorzino, Endenna, Zogno near Bergamo, northern Italy.

Diagnosis. As for genus.

Description. The body is oblong-ovate, two to three times as long as wide. The mean length is 8·5 mm (minimum 6·9 mm, maximum 10·8 mm), and the mean width, measured at the widest point, is 4·7 mm (minimum 3·0 mm, maximum 6·5 mm). The head is wider than long (3:2), with the anterior margin produced at the median point, over the base of the antennae, which have a multiarticulated peduncle and a flagellum composed of at least fourteen articles, reaching the posterior margin of the first thoracic tergite. The antennules and the eyes are unknown. The first tergite of the pereion is the longest, tergites II to IV are shorter and subequal, tergites V to VII are the shortest and again subequal. The epimera are large, rhomboidal and clearly distinct from the tergites. They point backwards, extending beyond the postero-lateral angle of their respective tergites. However, the first one reaches only to the posterior edge of its tergite. The last two epimera are posteriorly more rounded than the others. The pereiopods are ambulatory. The pleon is formed by two units, the first of which is as long as the first pereionite and shows four suture lines in the lateral regions. Lateral ends of this anterior unit project backwards and reach half the length of telson. The telson is usually subtriangular with a rounded posterior tip. A median ridge is present; it widens in the posterior third of the telson itself, expanding into a tubercle. Two large, elongate elevations flank the anterior part of the median ridge. Each also bears a tubercle at the posterior end. The uropods are biramous, the two branches of equal length. They are shorter than the telson, reaching about the posterior third, and have smooth margins and a rounded apex. The uropodal exopod is narrower than the endopod.

In a few specimens the shape of the telson is slightly different, being more rounded, without a protruding posterior tip; the ridges are less evident and the whole surface is covered by several relatively large pits. The uropods are somewhat longer. Differences detected in the telson shape and ornamentation may be interpreted as due to sexual dimorphism, even though this is not common in extant sphaeromatids.

Each thoracic tergite shows a row of about twenty round pits near the anterior margin. Behind each pit, there is a longitudinal depression, which does not reach the posterior edge. A few scattered shallow, round depressions are present on the telson. The whole surface of the body bears a fine micro-ornamentation (Text-fig. 2A–B). The shape of the microtubercles varies, relative to the position on each single pereionite: the anterior part is covered by domed, round granules, while the posterior one bears flat, transverse elements.

The cuticle is composed of two reticulate sheets (Text-fig. 2C) whose meshes can vary in shape from polygonal to very elongate.

Discussion. Among the several characters diagnostic for this family, only the pleon structure is easily detected on fossil material. The pleon itself is made up of only two units, the first formed by the fusion of the five anteriormost pleonites. In modern genera, three transverse sutures are usually present on this element, often only in the lateral regions (Naylor 1972). Because our specimens show clearly a single anterior pleonal unit, with four incomplete suture lines, we are confident that they belong to the Sphaeromatidae. Furthermore, we compared the microstructure of one of our specimens to that of an extant sphaeromatid (*Cymodoce*), and a few other isopod genera belonging to the Cirolanidae (*Cirolana* and *Aega*) and Gnathiidae (*Gnathia*). Similarities between *Triassphaeroma* and *Cymodoce* are striking, both showing an inner lattice of skeletal material (Text-fig. 2C–D). The other genera studied have a smooth or punctate surface, as observed by Wieder and Feldmann (1989) in the cirolanid *Palaega* Woodward, 1870 (= *Bathynomus* Milne Edwards, 1879), but have a fibrous inner structure.

Even if phylogenetic relationships with Recent sphaeromatid genera cannot properly be established, we find close affinities between our new genus and the extant genera *Sphaeroma* Latreille, 1804 and *Exosphaeroma* Stebbing, 1904, especially in the shape of pleotelson and the size of uropod. Fossil species placed in *Sphaeroma* are too poorly preserved, or show details of the pleotelson that do not allow their attribution to the genus (Van Straelen 1928). A few fossil genera are known; following the suggestion of Hessler (1969, p. R374), we compare our Triassic material mainly with them.

Isopodites von Ammon, 1882, is the only other sphaeromatid-like isopod from Triassic strata. It is very different from all other genera in having a very elongate cephalon. The short first pleonal unit with no traces of sutures, and the thin uropods which are much longer than the telson, are further characters distinguishing *Isopodites* from our specimens. *Eosphaeroma* Woodward, 1879 (from the Oligocene) is the fossil genus closest to our material in morphology. According to Van Straelen (1928) *Eosphaeroma* can be considered a 'basket genus' for the sphaeromatid-like isopods from the Cainozoic. Apart from differing in age from the new material (which is of limited significance in such a slowly evolving group), *Eosphaeroma* is very different in most diagnostic characters useful for the palaeontological taxonomy of this group; these are cephalon shape and dimensions, first pleonal unit structure, shape of the telson and relative length of uropods. All other fossil genera are very distinct from *Triassphaeroma* in shape and body proportions (Hessler 1969; Iverson and Chivers 1984).

Family SEROLIDAE Dana, 1852

Discussion. Fossil serolids are very rare: apart from *Elioserolis* gen. nov., only *Anhelkocephalon* tentatively can be ascribed to this family (Schwebel *et al.* 1983) on the basis of the enlarged telson, as suggested by Bill (1914), whose description of *A. handlirschi* was based on specimens from the Triassic Voltzia Sandstone of the Vosges. However, neither a diagnosis or an illustration was given. Bill (1914) erected his taxon on the following characters: cephalon deeply embedded in the first pereionite, a reduced number of pleionites, and a large telson. On this basis *A. handlirschi* is only identified as a serolid-like isopod. Von Straelen (1928) was unable to locate the holotype at the Institut de Géologie de Strasbourg, and doubted if *A. handlirschi* should be included in the Serolidae. According to Schwebel *et al.* (1983), Bill's specimens were lost in a fire at the institute in 1967, and they redescribed the species using new material and selected a neotype. The latter is 30 mm long, while a second specimen is less than 8 mm long; both are known only from the ventral side. The main difference from the original description (Bill 1914) concerns the head; in ventral view 'le cephalon parait nettement degagé du pereion' (Schwebel *et al.* 1983, p. 308). However, we cannot exclude the posterior dorsal fusion of the cephalon with the first pereionite, so that the old (Bill 1914) and new (Schwebel *et al.* 1983) descriptions may be compatible.

Because Bill's specimens were in dorsal view, and those of Schwebel *et al.* are both in ventral view, a confident attribution of the latter to Bill's species is difficult, because characters visible on the dorsal and ventral sides cannot precisely be related to each other. However, since all the material comes from the same horizon, it could well belong the same taxon. Bill's vague original description of *A. handlirschi* easily encompasses our fossils, but this is not the case for the neotype of Schwebel *et al.* (1983). The telson proportions of the latter are very different from our material, as well as from those of all living serolids.

Hessler (1969, p. R379) gave the following diagnosis for the Serolidae (here quoted only for characters usually visible on fossil material): 'body strongly flattened and broad, cephalon sunk deeply into first pereionite and fused to it posteriorly; antennules and antennae both with well-defined peduncle and multiarticulate flagellum; epimeres of pereionite extensive; tergum of last thoracomere usually absent; pleon composed of four units, three relatively subequal pleonites and one large pleotelson; uropoda lateral, with free rami'.

More recently, Brandt (1988) gave a different interpretation of the dorsal segmentation of serolids, considering the reduced element once regarded as the first pleonite (Richardson 1905; Hessler 1969) to be a seventh pereionite. We are not convinced by this change of interpretation of living serolids; even early authors should not have had difficulty in finding the correspondence between thoracic limbs and tergites. A full review of this apparent contradiction is beyond the scope of this work; however, we must point out that in many other isopods the first pleonite appears dorsally reduced in the central region and laterally surrounded by the last pereionite, which is always complete in its lateral regions. Furthermore, in many serolids the last one or two 'complete' pereionites (*sensu* Brandt 1988) show a great reduction in the median region (see, for instance, *Heteroserolis australiensis* (Beddard, 1884) or *Frontoserolis waegelei* (Brandt, 1988)). An inversion of this reduction tendency in the last (seventh) pereionite (*sensu* Brandt 1988) seems very unlikely. Brandt (1988) also noted that in serolids the first three pleopods are similar; thus they would more likely belong to three free pleonites rather than to two as in Brandt's interpretation. The biphasic moulting recorded in *Elioserolis* gen. nov. also points to the presence of seven completely developed pereionites. In the light of these remarks, and from a palaeontological point of view, we prefer to follow Hessler's interpretation, considering the pleon comprising three free pleonites followed by a pleotelson.

However, the statement concerning the lack of the seventh pereionite on the dorsal side (Hessler 1969) seems to be in contrast with the clear evidence of seven complete and distinct thoracic tergites in some Recent species, as well as in our Triassic specimens. In Recent serolids, the first two tergites appear to be firmly fixed to each other or fused together, but with more-or-less evident suture lines, so that they are usually considered as one unit. In her diagnosis of *Ceratoserolis* Cals, 1977, Brandt

(1988, p. 34) wrote: 'Mediolaterally of head on both sides a shallow suture running almost parallel to the caudal margin of the first pereionite' and illustrated this feature in *Ceratoserolis pasternaki* (Kussakin, 1967) and *Serolis aestimabilis* Brandt, 1988.

In our interpretation, the seventh tergum does exist, the reduction (fusion) taking place in the two most anterior ones. The Triassic specimens show seven pereionites, as in our interpretation of Recent *Serolis*, but they are all completely free. We regard this as a reflection of the relative primitiveness of *Elioserolis* gen. nov. compared to *Serolis s.l.* This is in agreement with the general evolutionary trend of Crustacea toward a reduction of the number of free thoracic segments. Thus, we feel confident that *Elioserolis* gen. nov. can be ascribed to Serolidae, in spite of its free first two pereionites. We therefore emend Hessler's (1969) family diagnosis, as it applies to the number and development of the pereionites, as follows: Serolidae showing seven complete pereionites, at least in the lateral regions; the first two may be free or fused with a more or less visible suture.

Genus ELIOSEROLIS gen. nov.

Derivation of name. For Professor Elio Robba, Università degli Studi di Milano, with the suffix *serolis*.

Diagnosis. Medium-sized (up to 12 mm) serolid; body outline broadly oval; cephalon deeply embedded in the first pereionite (dorsal view); pereionites with obtusely rounded antero-lateral angle, well protruded postero-lateral ends and triangular expansion in the middle of lateral posterior edge; three pleonites, the first of which is reduced; subtriangular telson.

Elioserolis alpina sp. nov.

Text-figure 3

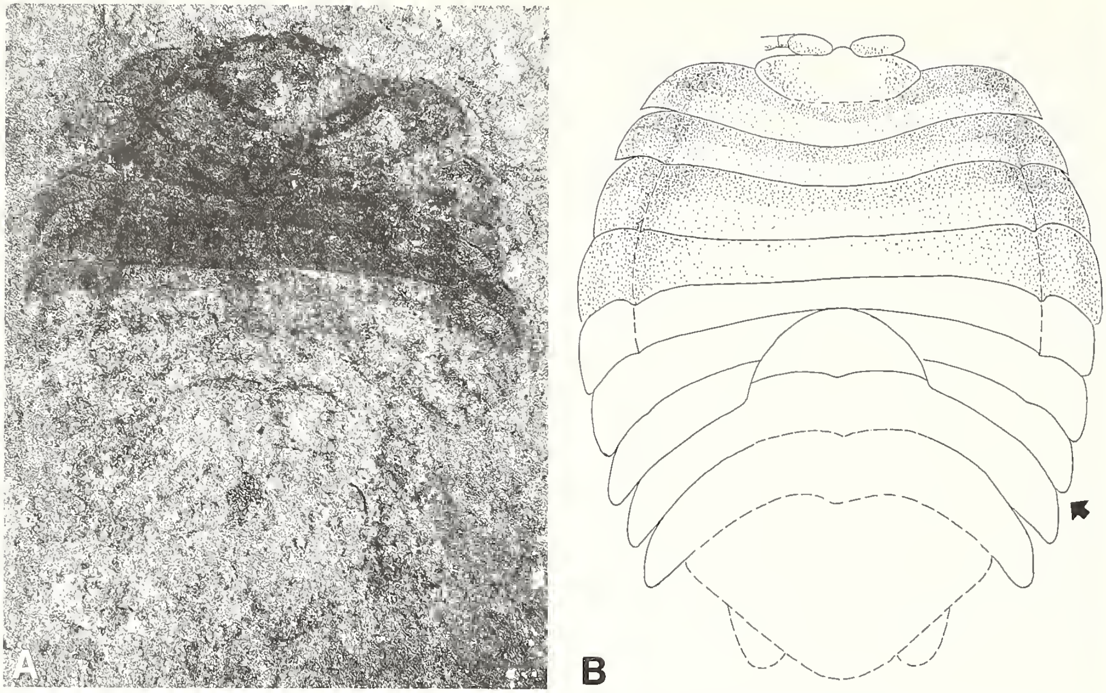
Derivation of name. From the Alps, where the specimens were found.

Types. Holotype MPUM 7036 in dorsal view, part and counterpart; paratype MPUM 7037 in ventral view, incomplete on its left side. The only other known specimen. Both from Calcare di Zorzino, Zogno 2, Bergamo, northern Italy.

Diagnosis. As for genus.

Description. Body broadly oval, narrower than long, the holotype being 11 mm long and 9 mm wide. The second, incomplete, specimen is somewhat larger. The cephalon is hardly distinguishable from the pereionite in which it is sunken. The antennae are articulated, with the first article of the peduncle about 0·5 mm long. The preserved part of the peduncle itself is about three times as long as wide. Only three flagellum articles are visible on the left antenna. The pereion shows seven somites, the first of which encircles the cephalon. The following four are similar, while the seventh is greatly reduced in its median region, where it appears to be fused with the sixth. Pereionites are dorsally expanded, the coxal plates being fused to the corresponding tergite. The antero-lateral angles of each pereionite are obtusely rounded, while the postero-lateral ends project backwards. The posterior edge of the first three pereionites shows a small, triangular expansion near the insertion of the coxal plates. The mineralization is markedly lighter in pereionites V–VII. All pereionites are divided transversely by a thin line marking a slight difference in mineralization between the anterior and posterior part. In the first three pereionites this line runs parallel to their posterior margin. Posterior to the pereion, three short pleonites are visible, the posterior two with well-developed epimeres. The first pleonite is reduced in the central region, as in modern serolids, and also shows a posteriorly directed median tip. The other two are complete. The light mineralization prevents a clear view of the pleotelson region, but traces of a fourth pleonal segment are still visible in the lateral region, perhaps partially fused to the pleotelson itself, as is the case in modern serolids. The pleotelson seems to be subtriangular, with a rounded posterior tip. Legs are robust and ambulatory, with dactylus curved and much thinner than propodus. All leg podomeres bore dense setae.

Mineralization of both specimens is heavy in the anterior region (head and the four anteriormost pereionites) whereas it is very light in the last three pereionites and the pleon. As suggested above, this can be related to the biphasic moulting which occurs in most isopods (George 1972). As George (1972) pointed out, the ecdysis



TEXT-FIG. 3. *Elioserolis alpina* gen. et sp. nov. A, MPUM 7036a, holotype; Calcare di Zorzino; Zogno 2, Bergamo, northern Italy; note the much more mineralized anterior region showing four free pereionites and the crescentic reduced first pleonite; ×10. B, restoration in dorsal view; the arrow points to the boundary between the pereion and the pleon.

of the posterior half (the three posteriormost pereonal somites plus the pleon) precedes that of the anterior. Thus, two-phase moulting had already evolved by Triassic times, at least within serolids.

CONCLUSIONS

Although caution is needed when comparing fossil and living species (Hessler 1969), strong similarities have allowed the new Triassic isopods to be assigned to Recent taxa, at least at supra-generic rank. *Triassphaeroma magnificum* belongs to the Flabellifera, a group encompassing several fossil taxa. Our material can confidently be ascribed to the Sphaeromatidae on the basis of both morphological analogies and exoskeletal ornamentation and microstructure, the latter being the first described from fossil isopods.

The stratigraphical range of Serolidae is extended back to the Triassic; *Elioserolis* is the only definitive fossil representative of the family. Seven free and laterally complete pereionites are present, so that we can consider *Elioserolis* as the most primitive serolid, the extant ones showing different degrees of fusion of the first two dorsal segments. On the basis of this character, the diagnosis of the family Serolidae has been emended. A bi-phasic moulting style, as observed in most modern isopods, is also recorded. An analysis of evolutionary phenomena involved in the origin and dispersion of Serolidae has been given by Brandt (1992*a*, 1992*b*). She concluded that 'the centre of origin of the family lies in a cold-temperate Gondwana province' (Brandt 1992*a*, p. 419). She also hypothesized a shelf habitat for primitive species, while derived relatives appear to be distributed in the deep sea, thus providing evidence of an onshore–offshore migration. *E. alpina* inhabited a sub-tropical intracarbonate platform basin in western Tethys during the Triassic. Thus, the problem of localizing the centre of origin for the geographic dispersal of the Serolidae can be seen in a new light. The family is much older than the previously supposed 90 Ma (Brandt 1992*a*), extending back for over 210 Ma.

Though no other fossil serolids are known in the interval between the Triassic and today, we can speculate that the primitive dispersal centre lay in westernmost Tethys, which had a rather warm environment. The opening of the central and southern Atlantic during Jurassic and Cretaceous times may have led serolids to migrate southwards along the continental shelf of South America, from warm to cold waters. They could have colonized the southernmost region of the Atlantic before South Africa separated from the block comprising South America, Antarctica and Australia, supporting the present day, mainly southern, distribution. Thus, serolids in the Caribbean region could be regarded as a relict primitive population rather than a recent immigration from Antarctica as suggested by Brandt (1992*a*).

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A DRAFT SYSTEM FOR THE IDENTIFICATION AND DESCRIPTION OF ARTHROPOD TRACKWAYS

by NIGEL H. TREWIN

ABSTRACT. The general morphological features of arthropod trackways are defined under headings of trackway width, imprint morphologies, track rows, repeat distance, symmetry, continuous marks, discontinuous marks and trackway curvature. These features are combined in a standard format for use in trackway description and diagnosis. The data can be used in a Trackway Data System, in which trackway attributes are represented by a formula of numbers and letters. The establishment of such a system and associated database would be a useful aid in identification and comparison of trackways using computer-based grouping or by construction of an Expert System. However, many genera will require redefinition and description before a sufficiently detailed database can be established.

ARTHROPOD trackways form a part of many trace-fossil assemblages, and pose particular problems for description and assignment to an ichnogenus. Many of the diagnoses in the literature are inadequate, in that they are either so general that they can accept a wide range of material, or else they contain such specific restrictions that the erected genus is likely to remain monospecific. Whilst the following analysis is applied to arthropod trackways, it could also be applied to the trackways of polychaete annelids.

There is no consensus on a preferred hierarchy of the elements composing a trackway, thus features such as size, imprint shapes, imprint series and continuous drag marks may be singled out, whilst other features are not included in description or diagnosis. A few publications deal almost exclusively with trackways. These include the privately published work of Smith (1909) and the revisions and descriptions of these Devonian traces by Walker (1985). Work on dominantly Permian traces by Walter (1983) introduced numerous new trackway names and a valiant attempt to order trackways into 'groups'. Hence he divided the Cursichnia (running tracks) of Müller (1962) into Multipodichnia, Pentapodichnia, Tetrapodichnia and Tripodichnia; placing greatest importance on the number of imprints occurring in groups or series in a trackway. Within these groups, Walter included or erected a number of genera and species. Müller (1962) extended the ethological classification of trace fossils by Seilacher (1953) to present a major group Movichnia (movement traces) which he subdivided into four sub-groups representing flying (Volichnia), swimming (Natichnia), running (Cursichnia) and crawling (Repichnia). In practice, it is frequently difficult to decide in which subgroup to place a trackway, and this classification is of more use for academic discussion than as a practical classification of traces. Similarly the complex classification scheme of Vyalov (1968) (summary in Häntzchel 1975) has not been adopted as a practical system. This contribution is not concerned with the question of classification, but with the problems associated with description and diagnosis of trackways in the broad sense.

It is generally at genus and species level that difficulties arise due to inadequate designations or restrictive designations based on one or two specimens. Such designations need to be constructed with sufficient latitude and clarity to provide a useful taxon, but not with such restrictions that make it unlikely that another trackway would ever be placed in that taxon.

The purpose of this contribution is to summarize the characteristics of trackways that should be included in descriptions and considered for diagnoses; and to provide a report form for use in trackway description, and in diagnosis construction. A machine-readable Trackway Data System

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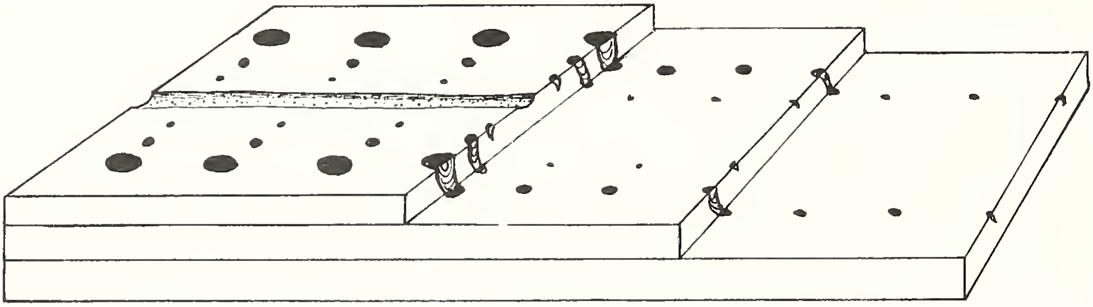
which reduces the main attributes of trackways to a simple formula is also introduced, and discussion is invited on the system before a working database is established.

TRACKWAY PRESERVATION

Prior to description of trackway components, it is necessary to consider the preservational aspects of the problem. Ichnotaxa are based on morphology and not on the originator; thus different preservational expressions of a track made by the same animal when walking on dry or wet sand, mud or silt, or in or out of water, will frequently fall in different taxa. Rolfe (1980) illustrated the marked differences in trackways of millipedes walking on wet mud and dry powder, and Sadler (1993) discussed differences in scorpion (*Hadrurus*) and spider (*Aphonopelma*) tracks on dry and damp sand. Experiments reported by Manton (1973, 1977) are most instructive in showing changes in gait and resulting trackways associated with speed of the animal, but trackways made on smoked glass cannot directly be compared with those on mud or sand. Appendages may be dragged in wet conditions but make discrete prints on a dry surface. In order for any impression to occur, the appendage must break the surface, and circumstances occur where only the heaviest foot-falls of the animal break the surface, the lighter ones leaving no impression. Temperature may even affect the activity and hence trackway of an arthropod, as observed by Brady (1947) in the case of the scorpion *Centruroides*. Thus, not every apparently well preserved trackway necessarily gives evidence of the number of legs used in locomotion.

Tracks commonly occur as epichnial impressions or can be moulded as convex hypichnia, and hence definitions of grooves or ridges must specify the preservation. It is recommended that trackways be described with respect to their epichnial preservations. A trackway may change character markedly along its length, maybe due to change of substrate or a change in the activity of the animal. To avoid a plethora of names relating to the same track, it is proposed that the naming of the trackway should refer to the highest level of organization recognized, which is clearly repeated along the trackway. This practice has been followed effectively by authors with abundant material to study, thus Anderson discussed variation in *Petalichnus* (Anderson 1975) and *Umfolozia* (Anderson 1981) and avoided the creation of numerous supposedly new genera and species.

Trackways may also be preserved as undertracks and the more lightly impressed elements of the surface trackway may not be preserved in the undertrack (Text-fig. 1). Ideally, undertracks should not be given new generic names but be described as, for example, 'undertrack of *Paleohelcura*'. In practice it can be difficult to identify a specimen as an undertrack, and many have received names. Clearly, all morphologically distinct trackways should initially be named and described; later it might be shown that they are undertracks or some other preservational aspect of another trackway.



TEXT-FIG. 1. Diagram illustrating the variation of a hypothetical trackway in undertrack preservation due to different depths of impression of appendages.

TRACKWAY COMPONENTS

The following breakdown of trackway components into eight sections follows, with additions, the work by Seilacher (1955) and Walter (1984). The terms used are illustrated in Text-figure 2. In trilobite work, a trackway may be referred to as a trail (e.g. Osgood 1970), but trail should be reserved for ribbon-like continuous traces lacking discrete leg imprints. Problems of definition do arise since trackways with defined prints can grade into ribbon-like traces as the maker moves from a damp to a wet substrate. Trilobites could plough through the surface sediment to leave *Cruziana* trails, or walk to give trackways. Clearly there is a gradation and definition becomes difficult, particularly since an arthropod may leave a continuous drag mark in addition to clear imprints. Such combinations are described here as trackways.

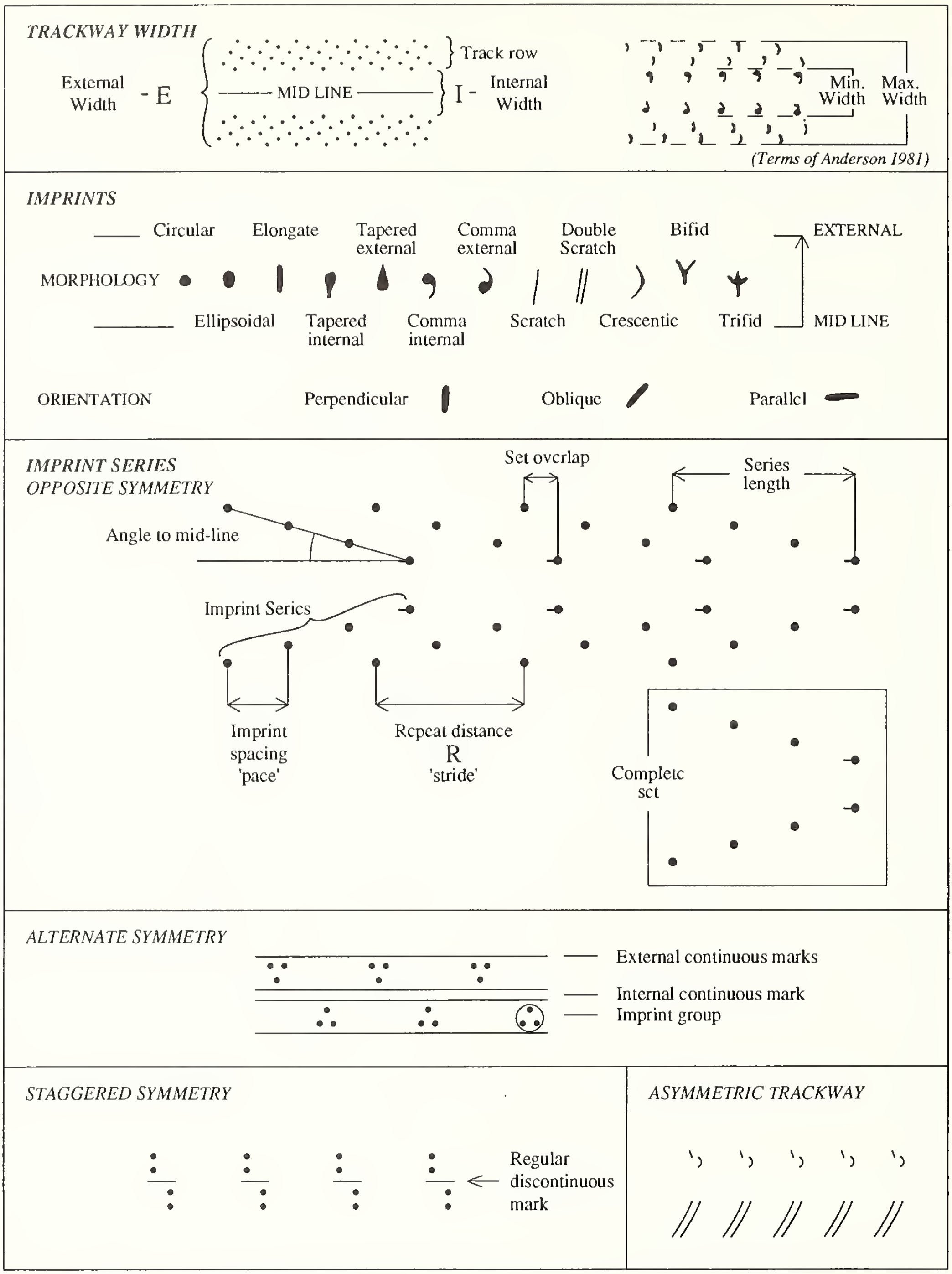
1. *Trackway width* (Text-fig. 2). In most trackways external and internal widths can be measured. In both cases it is useful to establish the range and mean of these values (e.g. Pollard 1985) and also to express them as a ratio. It is generally advantageous if absolute size is not used as an ichnogeneric discrimination, since this opens the way for unnecessary new genera, or may necessitate revision of diagnoses when identical material of a different size range is discovered. If the individual prints are elongate more detailed measurements can be made using the outer or inner extremities of prints within imprint series. In Anderson's (1981) study of *Umfolozia*, a minimum width at the outer extremity of the print pairs nearest the mid-lane was measured. Thus, internal width differs from minimum width (Text-fig. 2).

2. *Imprint morphologies* (Text-fig. 2). An imprint is the mark made by an element of a single appendage. This is frequently a locomotory appendage, but other parts of the animal may make regular imprints. Imprint morphology and orientation are frequently extremely variable within individual trackways. This can be the result of different character and action of appendages, or change in animal activity, or change in substrate. Where imprint shapes within a single trackway are highly and continuously variable in shape and orientation they have little potential for useful taxonomy. However, impressions of appendages bearing distinctive structures, such as bifid or trifid claws, provide useful diagnostic evidence. Osgood (1970) uses the terms proximal and distal (relative to the midline) in the description of imprint morphology. The presence of push-up mounds of sediment at the rear of leg imprints, or tic marks left by the drag of departing legs (Sadler 1993) may reveal the direction of motion, but caution must be exercised and it is frequently impossible to determine direction of motion. Thus the interpretation of direction of movement should not be part of the definition of the trackway.

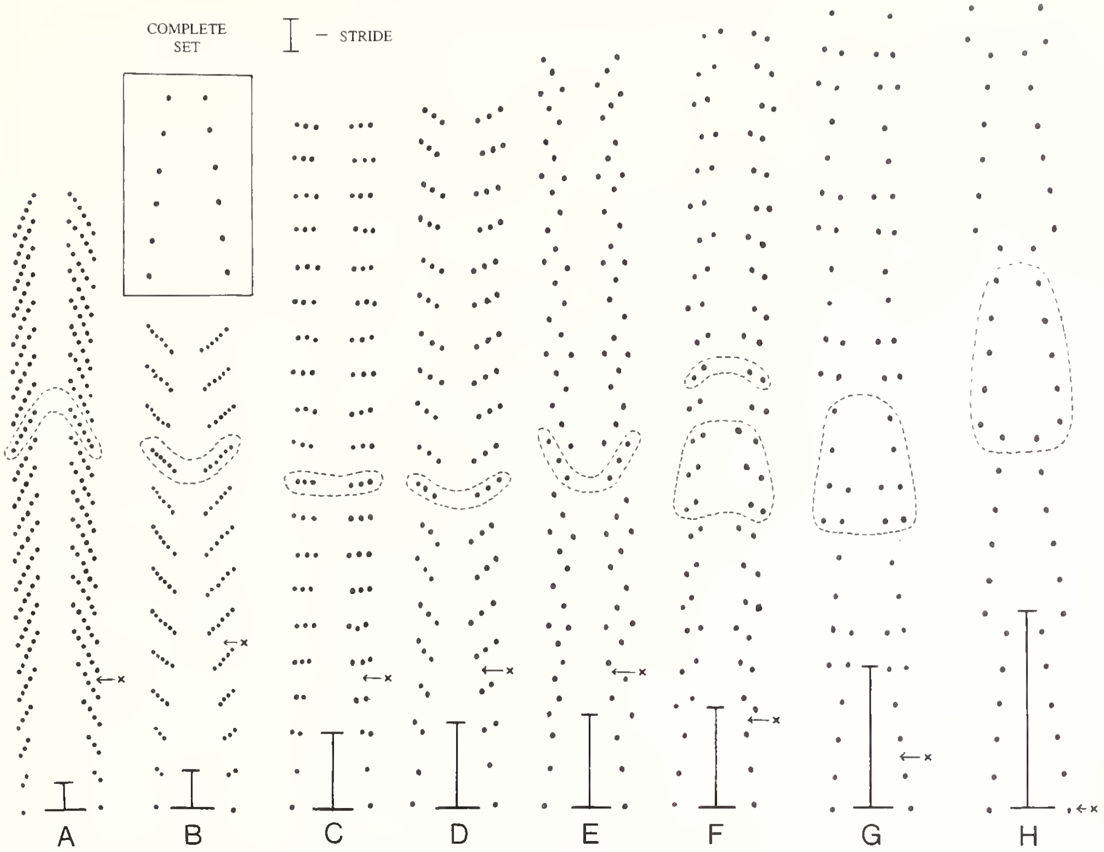
3. *Track Rows*. Recognition and interpretation of organization within track rows is important both for description and for interpretation of trackway originators. This was clearly recognized by Seilacher (1955) and Osgood (1970), and was used by Walter (1983) in his trackway classification.

Track rows can be regarded as simple (single row of imprints) or compound (several imprints in width of track row). The recognition of imprint series or groups (Text-fig. 2) raises the organizational status of a trackway, and such organization should be an important part of the diagnosis. In many trackways, organization can only be recognized or interpreted with confidence at trackway bends. False or apparent groups may result from coincidences in repeat length.

The concepts of Imprint Series and Imprint Groups can be confusing both from the requirements of description and interpretation. Series usually represent a movement phase of the animal using all appendages once, but groups do not necessarily represent the same situation. This feature is illustrated by Text-figure 3, which shows how trackway series can be wrongly described, resulting in a misinterpretation of the number of legs, morphology or gait of the arthropod. Text-figure 3 was constructed by taking a basic simple set of twelve prints, with series in straight lines at a low angle to the mid-line. Whilst this is a hypothetical set, it closely resembles those of *Petalichnus capensis* (nine to ten prints in a series, Anderson 1975) and *Umfolozia* (five prints in a series, Anderson 1981).



TEXT-FIG. 2. Diagram to illustrate the attributes of arthropod trackways and their terminology.



TEXT-FIG. 3. Hypothetical trackways produced by the repetition of a twelve-imprint set made of two oblique series of six. Repetition of the set upwards from the base of the figure using different repeat distances, or strides (the vertical lines) but with constant pace, produces a great variety of apparent, but false, series or groups, of which a few eye-catching examples are indicated enclosed in dotted lines. These false groupings mask the true nature of the complete set. The mark 'x' on each trackway represents the point at which the full pattern is developed by repetition of the set. Despite the somewhat artificial regular oblique nature of the imprint series of the set chosen, the results mimic closely effects seen in fossil trackways such as *Petalichnus* (in Anderson 1975) and *Umfolozia* (in Anderson 1981).

The trackways generated by variation of the Repeat Distance (the stride) are highly variable and produce false series or groups which can 'V' in either direction with respect to the mid-line and contain six, three or two prints (Text-fig. 3A–F). If both stride and pace are altered, further complexities arise. Only where there is little or no overlap between successive series does the true complete set become instantly recognizable (Text-fig. 3G–H). The experiments performed on living scorpions result in similar effects to those in Text-figure 3, as a result of differences in substrate, slope and activity of the animal (compare Sadler 1993, fig. 9).

The recognition of imprint groups is probably only valid for description in trackways which have an alternate or staggered symmetry. A pair of opposite imprint series was termed a complete set by Osgood (1970) and a triltsatz by Seilacher (1955). It is clearly important to recognize the form of the complete set if interpretations are made regarding leg numbers and direction of motion. Numbering of imprints within groups (e.g. Sadler 1993) may aid description, but imprint numbers will not generally relate to leg numbers on an arthropod, and are unlikely to be in a regular order with respect to leg number. In the terminology of Anderson (1975) a series would be a natural track cycle.

Generally, there will be an appropriate taxon for a trackway lacking recognized organization in groups or series, but when the organization becomes recognized (e.g. at a bend) the trackway would be elevated to another taxon (e.g. Pollard 1985, p. 278 – *Diplichnites* to *Acripes*).

4. *Repeat distance.* For the full description of a trackway, it is important to identify the repeat distance of the trackway, representing the stride of the animal (Text-fig. 2). This is generally obtained from the repeat distance of a distinctive imprint or imprint pair in the track rows. In view of the variable width of trackways within a species or genus, it can also be usefully expressed in relation to trackway width. Variation may be found representing different gaits of the animal associated with different activities (walking, stalking, feeding or running). Both stride and the distance between successive imprints (pace) might also vary due to external conditions, such as substrate type, and the force and direction of the wind or water currents. Identification of repeat distance and interpretation of imprint series is essential for analysis of arthropod gait (e.g. Briggs *et al.* 1979). The term repeated track cycle of Anderson (1975) is not required if the set overlap (Text-fig. 2) is identified and related to the complete set.

5. *Symmetry.* Many trackways have a symmetry about the mid-line (Text-fig. 2) which can be described as opposite (where opposite legs move in phase as in a looper caterpillar, millipede, notostracan or trilobite), or alternate (where at least three legs are on the ground at any one time as in a spider, scorpion or insect) or an intermediate staggered arrangement. The staggered arrangement may arise due to a normal gait on a flat surface, but could also be due to trackway distortion caused by the animal walking across a slope, or battling against the wind or a water current.

Some trackways are characteristically asymmetrical (Text-fig. 2) due to the activity of the animal (e.g. sideways motion of a crab, or dissimilar function of limb rows). Such intrinsically asymmetrical trackways require separate description of the track rows or, if they lack two well defined track rows, may have to be described as a single complex track row and an outer and inner side defined.

6. *Continuous Marks.* Continuous marks can be defined as those which continue unbroken along the trackway length for several repeat distances (Text-fig. 2). In some trackways, they are so persistent as to be used as a prime element of the diagnosis (e.g. *Siskemia* in revision by Walker (1985)) whilst in others they are less prominent or irregularly broken or preserved. Frequently they will only be apparent in a surface track, the undertrack showing no continuous impressions. They may be useful in determining the morphology of the animal, and the way it moved and turned corners (e.g. the classic *Siskemia* turning tracks illustrated by Smith (1909) and Pollard and Walker (1984)).

For descriptive purposes continuous marks can be described with respect to their position relative to track rows (internal, external) and their mutual spacing. Internal continuous marks may be related to ploughing of the head or drag of a tail. Constant spacing may indicate a telson with rigid spines, and variable spacing the drag of a pair of independently moveable spines. External marks, more usually discontinuous, may be made by spines on the margin of the head (e.g. genal spines of trilobites) or by thoracic spines.

7. *Discontinuous Marks.* Discontinuous marks may display a regularity associated with the repeat distance of the trackway (e.g. *Petalichnus capensis* in Anderson 1975) and may be due to repeated dragging of an appendage. On a soft surface appendages may be dragged through the surface to leave such a mark, but on a firmer surface only a simple imprint might result. Irregular discontinuous marks may only appear rarely along the length of a trackway, but nevertheless provide information on the morphology of the trackway maker. Their use in taxonomy is restricted by their irregular nature.

8. *Trackway Curvature.* The overall directional nature of the trackway (Text-fig. 2) can provide useful material for description or diagnosis, and information on the morphology and behaviour of the animal. Trackway curvature, minimum turning circle, abrupt angular direction changes, mutually oriented trackways and meandering style are all features worthy of consideration.

ILLUSTRATION OF TRACKWAYS

Clearly there is requirement for good quality photographic illustration. Such illustration should also encompass the range of form of the ichnogenus or species being described and defined.

In view of the difficulty of lighting and photographing delicately impressed trackways on undulating surfaces, it is also suggested that photographs be augmented with drawings of both the actual trackway and the authors interpretation of the ideal form which corresponds with his diagnosis or description. This is frequently done, but seldom is any attempt made to illustrate range in variation, and the illustrated material of many species relies on a single specimen. The work of Anderson (1975, 1981) is an example of good practice, based on exceptionally well preserved material, and Sadler (1993) provides a well illustrated comparison between ancient and modern trackways.

DESCRIPTION REPORT FORM

The form (Text-fig. 4) presented here is an attempt to order trackway description. Whilst it is intended to maximize the information included in a description, it must be stressed that not all of the descriptive sections 1–8 on the form would need to be used in a diagnosis of an ichnogenus or species. The organization of the form is not intended to imply any hierarchy of features in terms of importance for generic or specific diagnoses. It is suggested below that numerical methods such as cluster analysis could be applied to the data, and hence an equal value is required for each variable.

DERIVATION OF A DESCRIPTIVE FORMULA

A further stage in the ordering of trackway descriptions and diagnoses is to produce machine-readable data which can be expressed as a simple formula. The descriptive framework of Text-figure 4 has been utilized to produce the Trackway Data System (Text-fig. 5), a checklist which enables all features to be reduced to a set of numbers and letters. Numbers represent the *Descriptive Sections* of Text-figure 4, and letters the *Attributes* (Text-fig. 2) within each section. The Attributes can be morphological (e.g. Text-fig. 5, Section 2.1) or contain chosen numerical ranges (e.g. Text-fig. 5, Sections 1, 3, 4). The ranges chosen have been based on a brief survey of described trackways in an attempt to produce ranges with practical application. The morphological characters (e.g. in Section 2.1) could certainly be expanded, but the addition of a category OTHER enables unusual characters to be written in. The number of possible variables on the form exceeds 120, and should be sufficient to describe and distinguish trackways.

Most formulae derived from this system will contain only a few of the Sections and Attributes present on the form and thus formulae are generally relatively simple. Text-figure 6 illustrates a few trackways and the formulae derived from them by use of the Trackway Data Sheet.

In using the Trackway Data System, it will often be found that a range in morphology of the trackway covers more than one Attribute, thus trackways with a width range of 20–80 mm would have the designation 1·1 B, C. Within the imprint morphology section, trackways will also frequently have imprints of more than one Attribute as illustrated on the Data Sheet.

In Section 3 of the form, simple track rows are those with only a single line of prints, which may or may not have recognizable series. Compound track rows have more than one imprint in the width of the track row; thus series overlap. In compound track rows, the number of imprints in a unit length of the trackway equal to its external width (E) can be counted. This is independent of size and can be counted in all compound trackways whether or not series or groups are described.

In Section 4, the Repeat Distance or stride is measured and related to the trackway width. Thus trackways with a repeat distance less than the trackway width (E) have values greater than unity

NAME

STRATIGRAPHY

LOCALITY

Preservation :

DESCRIPTION

1. Trackway Width : External (E) $\frac{E}{I} =$

   Internal (I)

2. Imprint Morphologies /
   and orientations

3. Track Rows :

   Simple A No Series

   B Series

   Compound A Not organised

   B Organised - Imprint Series

   C Organised - Imprint Groups

   D Form of 'Complete Set'

4. Repeat Distance R : $\frac{E}{R} =$

5. Symmetry :

6. Continuous Marks :

7. Discontinuous Marks :
   - A Regular
   - B Irregular

8. Trackway Curvature

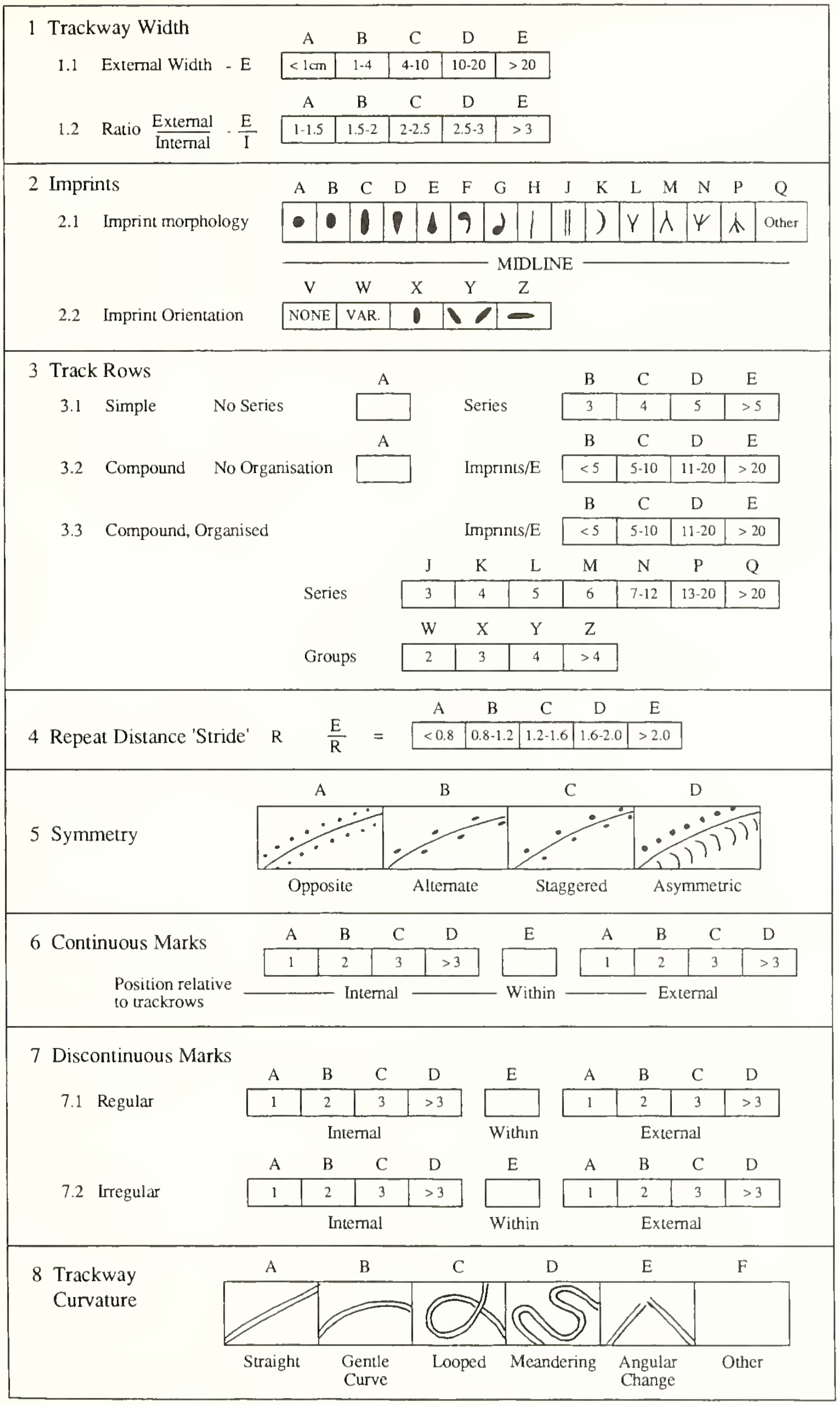
DRAWING - IDEAL FORM

DRAWING - TYPE

NOTES

COLLECTION AND NUMBER

TEXT-FIG. 4. Form for description of arthropod trackways (see text).



1 Trackway Width

	A	B	C	D	E
1.1 External Width - E	< 1cm	1-4	4-10	10-20	> 20
1.2 Ratio External / Internal - E / I	1-1.5	1.5-2	2-2.5	2.5-3	> 3

2 Imprints

	A	B	C	D	E	F	G	H	J	K	L	M	N	P	Q
2.1 Imprint morphology															Other

MIDLINE

	V	W	X	Y	Z
2.2 Imprint Orientation	NONE	VAR.			

3 Track Rows

		A		B	C	D	E
3.1 Simple	No Series		Series	3	4	5	> 5
3.2 Compound	No Organisation		Imprints/E	< 5	5-10	11-20	> 20
3.3 Compound, Organised			Imprints/E	< 5	5-10	11-20	> 20

	J	K	L	M	N	P	Q
Series	3	4	5	6	7-12	13-20	> 20

	W	X	Y	Z
Groups	2	3	4	> 4

	A	B	C	D	E
4 Repeat Distance 'Stride' R $\frac{E}{R}$ =	< 0.8	0.8-1.2	1.2-1.6	1.6-2.0	> 2.0

	A	B	C	D
5 Symmetry	Opposite	Alternate	Staggered	Asymmetric

6 Continuous Marks

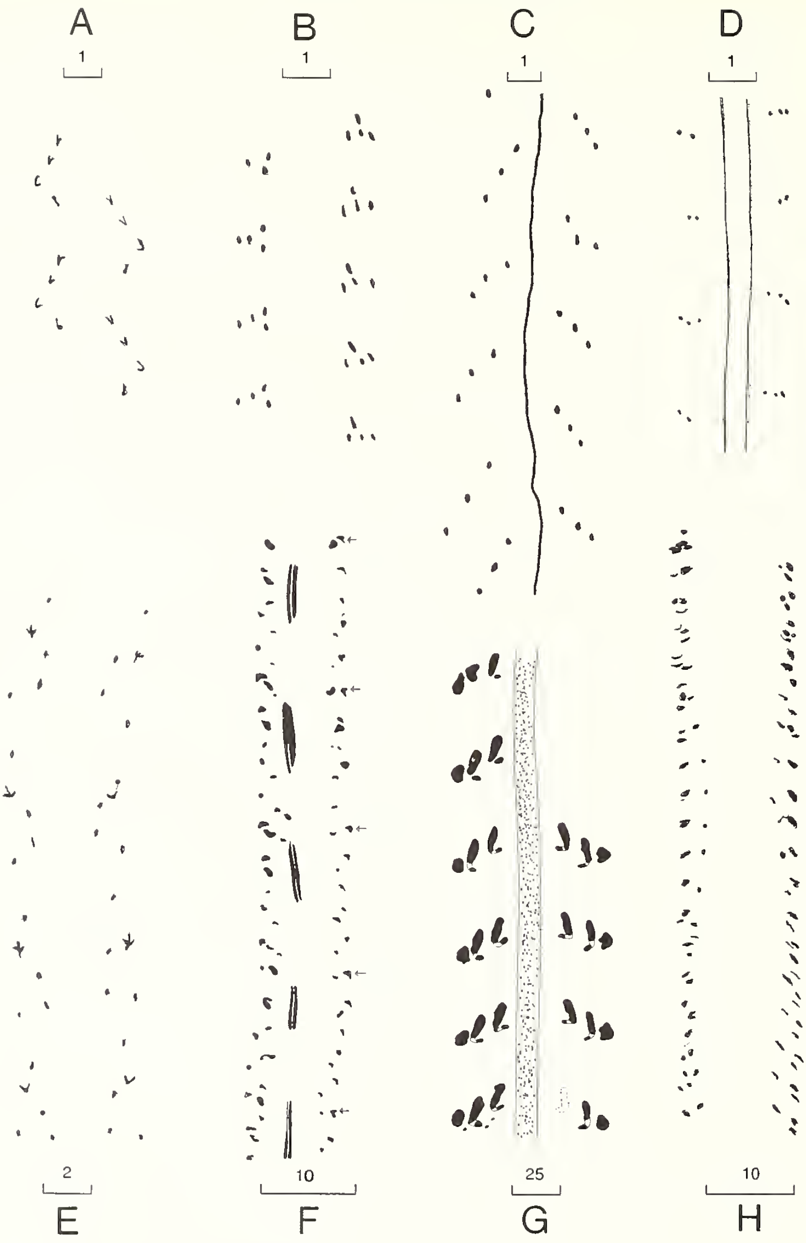
	A	B	C	D	E	A	B	C	D
	1	2	3	> 3		1	2	3	> 3
Position relative to trackrows	Internal				Within	External			

7 Discontinuous Marks

	A	B	C	D	E	A	B	C	D
7.1 Regular	1	2	3	> 3		1	2	3	> 3
	Internal				Within	External			
7.2 Irregular	1	2	3	> 3		1	2	3	> 3
	Internal				Within	External			

	A	B	C	D	E	F
8 Trackway Curvature	Straight	Gentle Curve	Looped	Meandering	Angular Change	Other

TEXT-FIG. 5. Form for the reduction of arthropod trackway descriptions to a format suitable for computer storage and comparison (see text).



Trackway Components	1		2		3			4	5	6	7		8
	1.1	1.2	2.1	2.2	3.1	3.2	3.3				7.1	7.2	
Trackways													
A	B	C	BL	Y	-	-	CY	B	B	-	-	-	A
B	B	B	B	YZ	-	-	DY	D	B	-	-	-	A
C	C	D	A	V	-	-	CX	B	B	A	-	-	A
D	B	B	A	V	-	-	WX	BC	C	B	-	-	AB
E	C	B	BN	ZY	-	-	CL	A	A	-	-	-	AB
F	CD	B	BCFGY	XY	-	-	DN	A	A	-	A	-	AB
G	E	D	ACM	Y	-	-	DJ	D	A	A	-	-	A
H	D	B	ABCDF	XY	-	AE	-	-	A	-	-	-	AB

TEXT-FIG. 6. For legend see opposite.

(Text-fig. 6B), and those with a repeat distance greater than the trackway width have values less than unity (Text-fig. 6E).

The main advantage of using such a system is that it greatly facilitates data comparison. This system could be utilized for simple cluster analysis programmes to show dissimilarity, and hence attempt a computer-based grouping. More usefully, it could be used to construct an Expert System whereby identifications could be made by the interrogation of the data base. At the simplest level this would enable anybody to request possible names for: 'a 30 mm wide trackway with two parallel internal grooves, track rows with circular and elongate imprints in groups of three with alternate trackway symmetry and a repeat distance of 25 mm'. The answer to such an input would come back as *Siskemia* Smith, 1909. As more data is input into such a system, it would become increasingly useful for the recognition of synonymies.

It must be stressed that the formula is not a substitute for a formal description or illustration, but it is an aid in the retrieval from a database of all trackways with similar features. Searches could thus be conducted for all trackways with features such as two medial grooves, imprint series of five, or trifid imprints. It has not been the intention to make the formula so complex that a trackway can be accurately drawn from the formula, but a close approximation could be constructed.

DISCUSSION

Proliferation of described ichnogenera of arthropod trackways is increasing present confusion of nomenclature. Many of the forms described in the early days of ichnology, and summarized and illustrated in Häntzschel (1975), are inadequately defined and illustrated in the original publications. Many genera are founded on very small numbers of specimens and intrageneric or intraspecific variation is not defined. If it was made a requirement that only five trackways of reasonable length (say with five set repeats) were needed to erect a new genus or species, the number of new descriptions would fall, but some interesting trackways would probably remain undescribed.

The number of variable features represented in the Description Report Form (Text-fig. 4) and the Trackway Data System can be combined to produce an enormous number of distinctive trackways, which many authors would consider of ichnogeneric or ichnospecific distinction. However, the proliferation of poorly described trackway ichnogenera does not advance our understanding of trackways, nor does it result in the scientific use of the bulk of existing names. The system proposed here is intended to reduce the number of genera and species to more manageable proportions.

Clearly, a drastic revision is required and this is probably outwith the scope (time and travel budget) of any individual. Inevitably revisions will be done in sections by interested individuals with taxonomic, palaeoenvironmental, or stratigraphical interests.

If genera are carefully described and non-restrictive revised diagnoses carefully constructed, the process of revision of trackway ichnogenera can proceed. It is hoped that the use of standard descriptive terms and the Trackway Data System will allow simple keys and computer aided systems for generic and specific identification to be constructed for trackway groups or stratigraphical formations, and ultimately for all arthropod trackways. The main drawback experienced by the author is the inadequate nature of illustration and description of many named forms. The system

---

TEXT-FIG. 6. Examples of trackways and their description formulae as derived from Text-fig. 5. A, *Octopodichnus didactylus* Gilmore, 1927; Arizona; Permian, Coconino Sandstone. B, *Octopodichnus raymondi* Sadler, 1993; Arizona; Permian, Coconino Sandstone. C, *Paleohelcura tridactyla* Gilmore, 1926 (from Brady 1947); Arizona; Permian, Coconino Sandstone. D, *Siskemia bipedicula* Smith, 1909 (from Walker 1985); Dunure, Scotland; Devonian, Lower Old Red Sandstone. E, *Kouphichnium* sp. Bavaria, Germany; Jurassic, Sölnhofen Limestone (author's collection). F, *Petalichnus capensis* Anderson, 1975; Brandenburg, Cape Province, South Africa; Ordovician, Table Mountain Sandstone (example with internal discontinuous mark – not present in all examples). G, *Palmichnium kosinskiorum* Briggs and Rolfe, 1983; Elk County, Pennsylvania; Carboniferous. H, *Diplichnites gouldi*, Western Australia; Silurian, Tumblagooda Sandstone; Western Australian Museum, No. 84.1634. All scale bars in cm.

advocated will thus require the cooperation of many ichnologists working to a common end by redescribing existing type material, and rejecting genera founded on material inadequate by modern standards.

I would welcome discussion and testing of this proposed system, so that it can be refined, if necessary, and grow into useful user-friendly database for ichnologists.

Acknowledgements. My thanks to all who have ever argued or discussed with me the names of arthropod trackways! Particular thanks to Ian Rolfe and John Pollard for many useful comments and suggestions on the original version. Barry Fulton patiently guided the figures through their evolution, and Karen Chalmers and Susan Simm processed the words.

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SILICEOUS DINOFLAGELLATE THECAL FOSSILS FROM THE EOCENE OF BARBADOS

by IAN C. HARDING *and* JANE LEWIS

ABSTRACT. Detailed sampling of Palaeogene sediments from Barbados has resulted in the rediscovery of the type locality of the rare siliceous dinoflagellate *Peridinites*. Electron microscopic examination has revealed that *Peridinites* can only be interpreted as the remains of dinoflagellate motile thecate cells, rather than hypnozygotic cysts; it thus represents the first unequivocal example of a fossil dinoflagellate theca. Dinoflagellate cysts have also been found and identified as belonging to *Lithoperidinium*. Both *Peridinites* and *Lithoperidinium* are valid genera, and are interpreted as being primarily silicified. *Peridinites* is thus the only known dinoflagellate capable of secreting siliceous thecal plates.

DINOFLAGELLATES may include in their life-cycles a motile stage (often a tabulated theca of cellulosic plates) and a resting cyst stage formed after sexual reproduction. The thecate motile stages are conventionally believed not to be represented in the fossil record, because of the volatile nature of the cellulose of which they are constructed (Allison and Briggs 1991). Dinoflagellate cysts, however, are usually composed of the complex biopolymer 'sporopollenin'; more rarely, additional calcareous layers are secreted. The dinoflagellate fossil record is conventionally envisaged as being almost exclusively composed of cysts.

Lefèvre (1933*a*) briefly described a new dinoflagellate genus, *Peridinites* (with seven species), from a single sample of Palaeogene radiolarite from Barbados. This is the more important of only two known genera of siliceous dinoflagellate body-fossils (a few motile cells such as species of *Actiniscus* (Ehrenberg) Ehrenberg, 1843 produce siliceous internal spicules); the second is *Jusella* Vozzhennikova, 1963. Additional species referrable to these genera have only been described from Russian borehole material (four species: Deflandre 1940; Vozzhennikova 1963, 1967) and New Zealand outcrop material (one species: Deflandre 1933). Finally, specimens which may be referrable to *Peridinites* were illustrated by Dale (1983), from material dredged from the Norwegian Sea. All specimens were isolated from poorly dated radiolarites or diatomites, none being better defined than of a 'Palaeogene' age.

Marine *Peridinites* displays the earliest known example of cinctioid tabulation, an organization characterized by an inverted pentagonal second anterior intercalary plate (Bujak and Davies 1983). Furthermore, it is not known whether *Peridinites* represents siliceous thecae, primarily siliceous cysts, or secondarily silicified cysts. It has been suggested (e.g. Bujak and Davies 1983, p. 34) that *Peridinites* was indeed primarily silicified, but no definite statement as to the cyst or thecal affinity of the fossil has been proposed.

The aim of this study was to employ high-resolution microscopic techniques to elucidate the detailed morphology of the fossils, and to identify the stage in the dinoflagellate life-cycle that they represent. The permanently mounted nature of the type material, held in the Deflandre Collection of the Museum d'Histoire naturel Paris, and the small size of the specimens (25–50 μm in diameter) necessitated the collection of new topotype material from Barbados.

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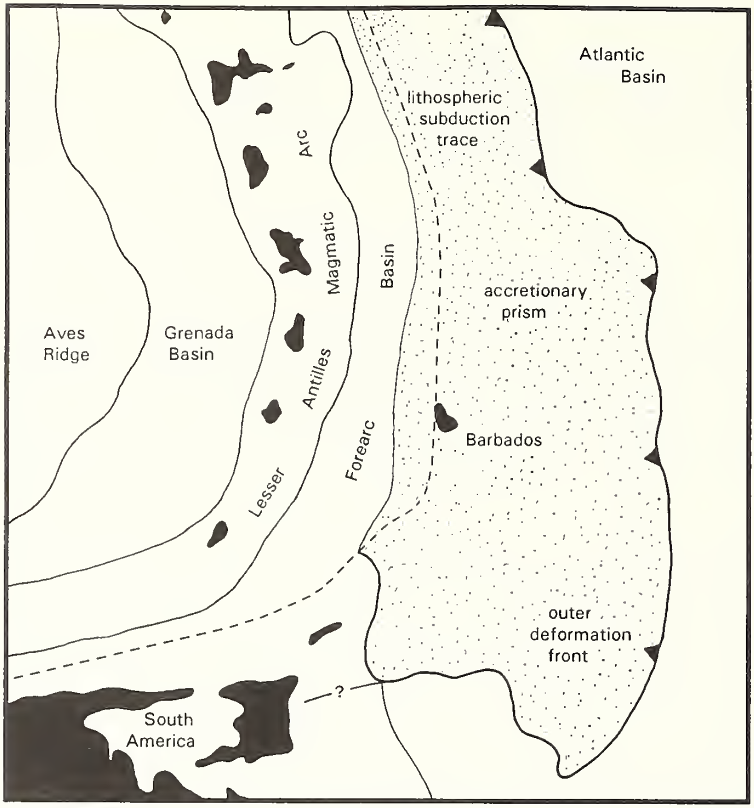


TEXT-FIG. 1. Geological setting of Barbados, showing the position of the outer deformation front of the accretionary prism and the inferred position of the subduction trace of the Atlantic plate (after Speed, 1983).

TYPE LOCALITY AND BARBADIAN GEOLOGY

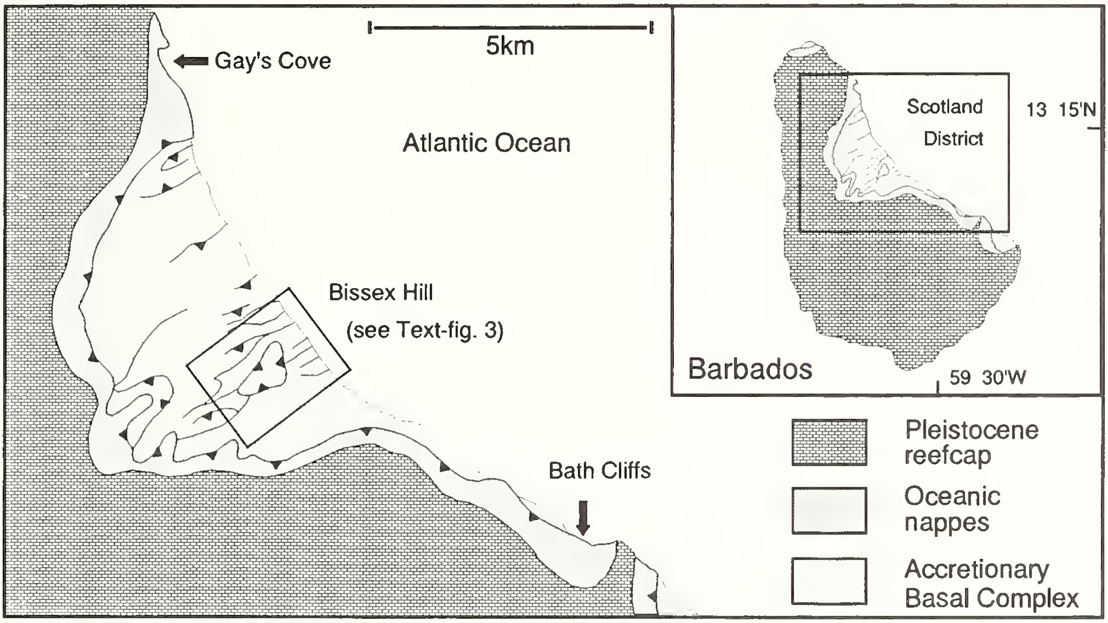
Type locality

The material examined by Lefèvre (1933*a*) in his original description of *Peridinites* was taken from collections of Barbadian material already held in the Laboratoire de Cryptogamie of the Museum d'Histoire naturel, Paris. The sample used for the original descriptions came from the collection of Petit, the vial of prepared material bearing the brief label 'Diatomées fossiles. Springfield, Barbades'. Subsequently, Lefèvre (1933*b*) discovered additional specimens in another set of samples previously prepared by Rataboul and Bourgogne. The greatest number of specimens was isolated from a tube labelled simply 'Barbades moyen'. No additional information is given in any of Lefèvre's papers regarding sample provenance. The present curator of the collections in the Laboratoire de Cryptogamie, Dr M.-T. Venec-Peyre, was unable to provide any further data which would aid in identifying the type locality or the date of sample collection. Examination of the type slides (by ICH) indicated that the type lithology was biogenic sediment rich in radiolaria, diatoms and sponge spicules.

Springfield (as on Lefèvre's label) is one of many sugar cane plantations on Barbados. Although the boundaries of these estates have been modified in recent decades, the name implies that the samples were probably collected in the vicinity.

Barbadian geology

During the period in which the samples were collected, Barbados was believed to have layer-cake stratigraphy (Jukes-Browne and Harrison 1892). More recently, the geology of the north-eastern quadrant of the island (known as the Scotland District) has been revised in the light of plate tectonic theory (Speed and Larue 1982; Speed 1985). Barbados is now known to be an emergent part of the Barbados accretionary prism, which lies above the descending North American plate, and eastwards of the Caribbean plate (Text-fig. 1). Springfield is located near to Bissex Hill, in the Scotland District (Text-fig. 2).

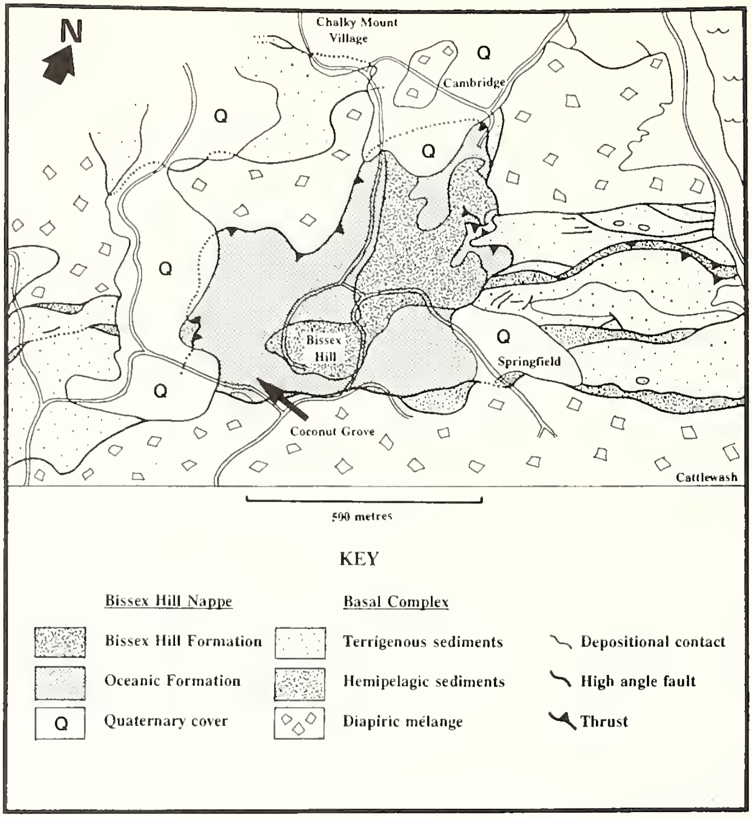


TEXT-FIG. 2. Inset shows island of Barbados, indicating northeastern Scotland District. Main map shows the geological units of this district and the location of Bissex Hill (after Speed, 1985).

The geological structure of the area around Springfield is complex, and consists of three main structural units (Larue and Speed 1984; Text-fig. 3). The first of these units consists of a series of east-northeast striking fault-bounded packets of sediments which form part of the basal accretionary complex of the island. Individual fault packets are composed of one of two lithological associations: a terrigenous suite (formerly known as the Scotland Series), and a hemipelagic suite (dominantly radiolarites, radiolarian mudstones and thin sandstones). Immediately to the west of Springfield lies the second structural unit, a subhorizontal thrust-sheet, the Bissex Hill Nappe, composed of calcareous biogenic sediments – the Oceanic Beds and the Bissex Hill Formation. These sediments have been backthrust over the Basal Complex from the Lesser Antilles fore-arc basic to the west (Text-fig. 1). The third structural unit is a diapiric mélange, formerly known as the Joes River Formation. The mélange is composed of mudstone, quartzose turbidite, radiolarite and calcareous pelagite clasts in a mudstone matrix.

Sample provenance

All the lithologies discussed above occur within 500 m of Springfield plantation house and, except for the terrigenous suite of the Basal Complex, could have yielded the specimens of *Peridinites*. A representative collection of samples from all lithologies cropping out in the vicinity of Springfield



TEXT-FIG. 3. Local geology around Springfield plantation house, northeastern Barbados, showing structural complexity of Basal Complex thrust slices overlain by Oceanic Nappe and intruded by diapiric mélange (after Larue and Speed, 1984).

was taken for examination. Samples were obtained from the hemipelagites of Packets 15 and 17 (of Larue and Speed 1984) in the Basal Complex, from the Oceanic Beds at Coconut Grove, from the Bissex Hill Formation on the summit of Bissex Hill, and also from clasts in the mélange (Packet 18). The specimens described here were isolated from the samples collected at Coconut Grove in the Oceanic Formation. These samples were buff-coloured, radiolarian-diatom pelagic oozes.

Radiolarian analysis (by ICH and Paul Robinson, Southampton) has dated the samples as being of mid Eocene age, belonging to the *Thyrsocyrtis triacantha* Zone (Sanfilippo *et al.* 1985; Pl. 1, fig. 8), on the occurrence of the eponymous species and *Theocotyle venezuelensis* Riedel and Sanfilippo, 1970. The siliceous component of the samples, although dominated by radiolaria, is also rich in centric diatoms and sponge spicules, with a similar species composition to the original type material.

MATERIALS AND METHODS

Various techniques were explored to determine the optimum methods for extracting the *Peridinites* fossils from the radiolarites, and a standard method used in the preparation of radiolaria produced the best results. Samples were broken into small pieces and soaked in Calgon (sodium hexametaphosphate) to break up the clay minerals; they were then decalcified using fifty per cent hydrochloric acid, followed by a treatment with ten per cent hydrogen peroxide to oxidize any obscuring organic matter. Samples more resistant to these treatments responded to gentle heating of the processing reagents. The rare specimens of *Peridinites* were concentrated by sieving into separate size fractions of > 125 μm, 125–63 μm, 63–40 μm, and 40–20 μm.

Peridinites proved to be most common in the 40–20 μm fraction, although they were still extremely rare, occurring at a frequency of approximately one siliceous dinoflagellate per 100000 radiolaria. The different size fractions were examined in distilled water using an Olympus BH–2 transmitted light microscope. Specimens were isolated by micropipette, and mounted on squares of film which were attached to aluminium electron microscopy stubs. Selected specimens were coated in carbon to allow X-ray compositional microanalysis to be conducted, in a JEOL JSM–6400 scanning electron microscope fitted with a Tracor Series II energy dispersive X-ray analysis system. Following analysis, specimens were sputter-coated with gold for photomicrography.

The specimens illustrated in this paper are housed in the Sedgwick Museum, Department of Earth Sciences, University of Cambridge, UK, under the catalogue numbers SM X.24547–X.24553.

RESULTS

Dinocysts versus dinoflagellate thecae

The features which can be used to discern a dinoflagellate cyst from a motile theca have been discussed by Dale (1983) and Evitt (1985) and are listed in Table 1. The specimens identified as belonging to *Peridinites*, fulfilled all of the morphological criteria required for the interpretation of *Peridinites* as fossils of the motile thecate stage in the dinoflagellate life-cycle.

TABLE 1. Comparison of morphological features found on motile dinoflagellate thecae and non-motile dinoflagellate cysts.

Peridiniacean motile cell features	Peridiniacean cyst features
Articulated plates	Continuous wall layer
Functional sutures	Non-functional parasutures
Plate overlap	Reflected overlap
Functional, depressed cingulum and sulcus	Often discontinuous ridges or grooves, ornamented areas, or not expressed
Functional flagellar pore	Flagellar scar
Trichocyst pores	Reflected pores, often represented as spines
Apical pore	Apical plate (P plate)
Ecdysal opening	Archaeopyle

1. The fragmentary nature of the *Peridinites* specimens is not due to mechanical breakage of the fossils (this can be seen around the cingulum of the specimen in Plate 1, figure 2) but rather to the dissociation of the individual siliceous plates of which the specimens are composed (see Pl. 1, fig. 4, Pl. 2, fig. 3). The fragmentation of the specimens followed lines of weakness along the boundaries between the individual plates and are not intraplate fractures. This implies that the junctions between the plates are functional sutures, rather than the thecamorphic non-functional parasutures found on some dinocysts (Gocht 1983), i.e. they are merely reflections of thecal features on the surface of the cyst. This is the most powerful argument for the interpretation of *Peridinites* as a motile thecate organism.

2. The plate overlap direction (Text-fig. 3A) is just as it would appear on the external surface of a modern theca. This contrasts with many sub-thecal fossil cysts, in which the paraplate overlap direction is inversely related to the plate overlap on the parent theca (Harding 1988).

3. The cingulum and the sulcus appear eminently capable of housing functional flagella, as

there are no obstructions along either, which would have inhibited normal flagellar function (e.g. Pl. 1, fig. 6).

4. Three types of pores are identified on *Peridinites*, which penetrate the siliceous wall from the external surface to the interior of the fossil (Pl. 1, figs 1, 5, 11). Whilst some dinocysts possess wall perforations (claustra) these never penetrate the hermetically sealed inner wall layer; such perforations are common in dinoflagellate thecal plates. In addition, a large pore is found within the apical horn (Pl. 1, fig. 12), of identical morphology to those found on modern peridinioid thecae (Dodge and Hermes 1981; Toriumi and Dodge 1993). A second pore-type is found at the convergence of cingulum and sulcus (Pl. 1, fig. 5) and presumably served for the emergence of a pair of flagella. The most common pores are interpreted as trichocyst openings, as their distribution in intraplate areas and lining the cingulum (Pl. 1, fig. 6) echoes their placement on modern peridinioids (Dodge 1983; Lewis 1990).

5. The sculpture of these fossils is particularly reminiscent of that of modern gonyaulacoids (Dodge 1989), although no systematic relationships are inferred by this.

6. Intercalary growth bands have not been observed on any of our specimens, although in the generic description of *Peridinites*, Lefèvre (1993*a*) described the occasional occurrence of transverse striations across the sutures. This is consistent with the interpretation of *Peridinites* as representing the motile stages of the life cycle, and including both vegetative thecae and zygotic thecae, as the latter display more prominent volume growth and thus wide intercalary growth bands.

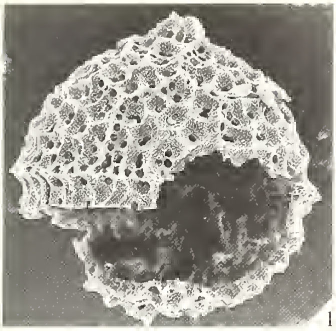
7. *Peridinites* displays a post-cingular opening formed by the loss of the three plates **2‴**, **3‴** and **4‴** (Pl. 1, fig. 4). If these specimens were vegetative thecae, their cell contents must have been able to escape from the cell during gametogenesis, a process known as ecdysis. Thus, rather than being excystment openings or archaeopyles, these features would be ecdysal openings. Although antapical archaeopyles have been suggested for three dinoflagellate genera (Wall and Dale 1971; McClean 1973), *Peridinites* is the only morphotype yet identified with an opening developed in the post-cingular plate series. An analysis of the plate overlap patterns of the epitheca revealed the second anterior intercalary to be the epithecal keystone plate, as is the case with modern protoperidinioids. Assuming that these siliceous thecae produced cysts, this observation suggests that the **2a** paraplate may have been involved in archaeopyle formation. The specimens of *Lithoperidinium oamaruense* Deflandre, 1933, and *L. rossicum* Deflandre, 1940 examined by ICH in Paris, and here believed to be of cyst affinity, do not contradict this statement.

EXPLANATION OF PLATE 1

Figs 1–7, 9–12. *Peridinites piriformis* Lefèvre; sample COC4; Coconut Grove, near Springfield, Barbados; Oceanic Formation, Eocene. 1–5, SM X.24547. 1, oblique dorsal view showing hypothecal ecdysal opening; note damaged **4″** and **5″** plates, and extensive development of trichocystal perforations in thecal plates; × 3000. 2, oblique right lateral view, showing damage to cingular and precingular **4″** and **5″** plates; × 3000. 3, antapico-dorsal view clearly showing the ecdysal opening resulting from the loss of plates **2‴–4‴**; × 3000. 4, antapical view illustrating the large hypothecal opening and the two small antapical plates; × 3000. 5, internal view showing large opening, interpreted as the flagellar pore, and smaller perforations, interpreted as trichocyst pores; note that pores penetrate the wall; × 7500. 6, SM X.24548; ventral view of isolated epitheca, note asymmetrical nature of plate **1′**, cingulum displaced by one cingulum width, and apical prominence; × 3400. 7, SM X.24549; internal view of isolated epitheca showing large apical pore with plate **3′** immediately above; note that the grooves parallel to the plate margins are only found on overlapping plate margins; × 6000. 9, SM X.24548; detail of plate **1″**, showing single rows of trichocyst pores along overlapped margins of plate **2′** at top of picture and plate **2″** to right of picture; × 6000. 10–12, SM X.24550. 10, apico-left lateral view, showing first precingular plate to left; × 3300. 11, apical view; note concentrations of trichocyst pores; first precingular plate to bottom; × 3000. 12, apical view of large, raised, open apical pore surrounded by trichocyst pore openings; note surface texture of fused silica granules; etched appearance may be due to incipient silica dissolution; × 15000.

Fig. 8. *Lithocytris vespertilio* Ehrenburg; sample COC4; Coconut Grove, near Springfield, Barbados; Oceanic Formation, Eocene; X.24560; × 370.

PLATE 1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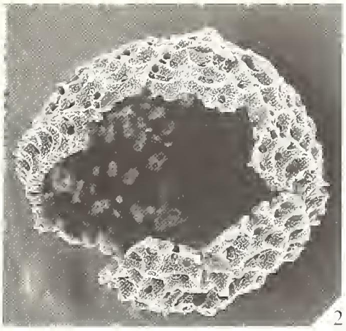
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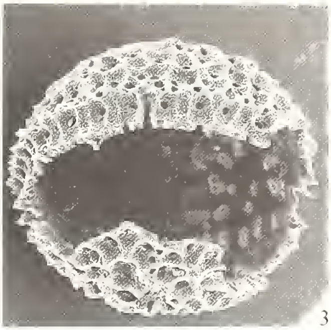
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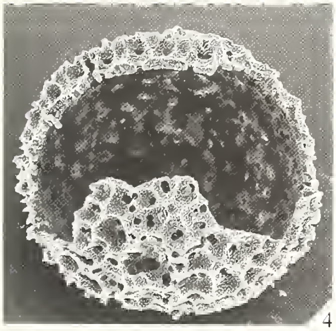
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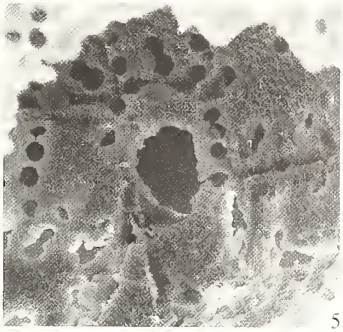
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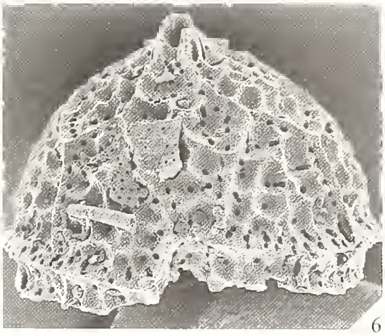
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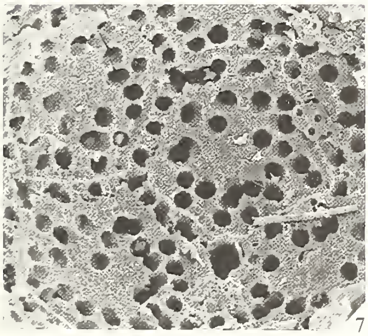
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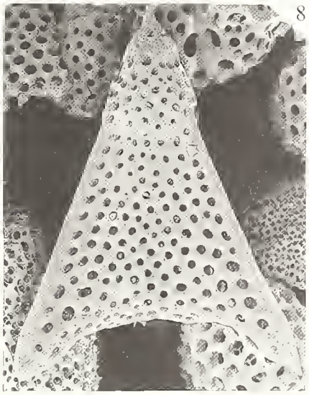

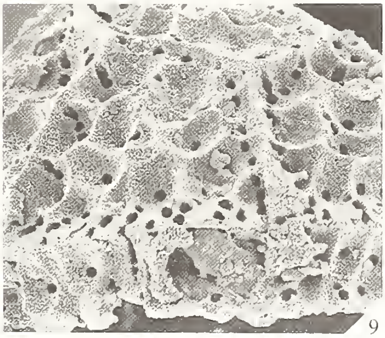
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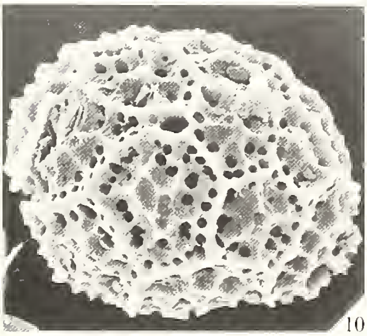
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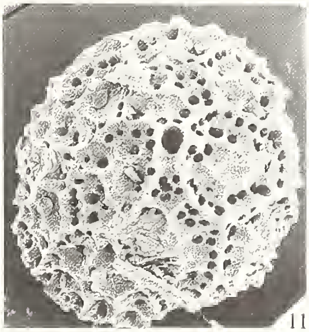
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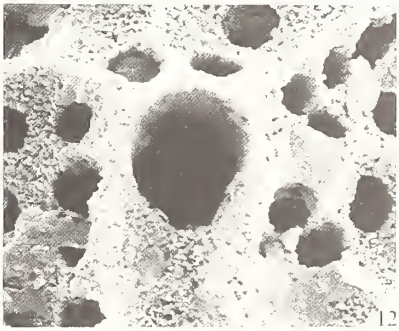
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HARDING and LEWIS, *Peridinites*, *Lithocytris*

In the authors' opinion, all of the features displayed by *Peridinites* are consistent with its interpretation as a motile thecate organism; indeed no morphological features have been discovered which would argue against this conclusion. After extensive discussion, Deflandre (1933) also concluded that this was likely. Thus, we interpret specimens of *Peridinites* as siliceous organisms, with morphological characteristics indicating they were motile thecate dinoflagellates. *Peridinites* is the only genus of unequivocal fossil dinoflagellate thecae yet identified.

Primary versus secondary silicification

X-ray microanalysis of *Peridinites* indicated an entirely siliceous composition. One modern dinoflagellate, *Thoracosphaera* Kamptner, 1927, produces mineralized vegetative cells (Tangen *et al.* 1982), but these are calcitic and not siliceous. Only the modern *Ceratium hirundinella* (O. F. Muller) Bergh, 1882 and *C. furcoides* (Levander) Langhans, 1925 secrete small siliceous granules on the external surface of their organic walled cysts (Chapman *et al.* 1982). All other dinoflagellates known to secrete silica do so in the form of internal sclerites (e.g. the star-shaped pentasters of actiniscids).

How then can the composition of *Peridinites* be explained? When described by Lefèvre (1933*a*, 1933*b*) *Peridinites* was believed to have been a secondarily silicified body fossil, a view also expressed by Balech (quoted in Bujak and Davies 1983, p. 34). However, Deflandre (1933) pointed out that they may have been primarily siliceous cells, a view supported by Bujak and Davies (1983, p. 34). Although difficult to prove, secondary silicification would need to be extremely rapid, prior to bacterial breakdown of the cellulosic plates. The samples all show indication of intensive bioturbation in well aerated bottom waters at the site of deposition, making such bacterial activity a strong likelihood. Indeed, it is unusual to encounter cellulosic dinoflagellate thecae in modern marine sediments (JL, personal observation). Furthermore, there is no evidence for the silicification of other volatile compounds in the residues, and the samples show no evidence of silicification of the well preserved calcareous microfossils, which co-occur in the topotype material. Examination of the siliceous component of the residues indicates active silica dissolution, especially of the more fragile centric diatoms, rather than secondary silicification. Thus, we interpret specimens of

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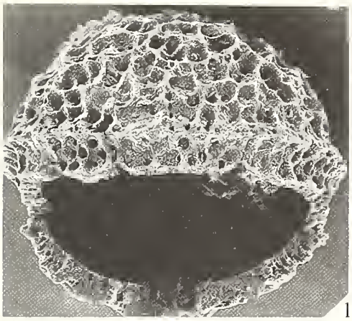
EXPLANATION OF PLATE 2

Figs 1–8. *Peridinites sphaericus* Lefèvre; sample COC4; Coconut Grove, near Springfield, Barbados; Oceanic Formation, Eocene. 1–5, SM X.24551. 1, dorsal view showing large hypothecal ecdysal opening and clearly functional sutures, especially between cingular plates; × 2700. 2, oblique left dorsal view showing low apical prominence and cinctioid **2a** plate with raised margins indicating overlap of all adjacent plates; × 2500. 3, antapical view showing ecdysal opening formed by loss of plates **2‴**, **3‴** and **4‴**; antapical and posterior sulcal plates have also been lost; note that all plates have separated along functional sutures; × 2500. 4, oblique left lateral view showing functional sutures between individual plates, large plate above the cingulum is 3″; × 3700. 5, detail of entire plate margins, indicating fragmentation of theca is due to separation of plates along functional sutures; plate margin at bottom of micrograph is the **1‴**/**2‴** suture, to the left is the cingulum/**2‴** suture; × 8000. 6, SM X.24552, detail of apical tabulation showing prominent apical pore, with **3′** to the right of this and cinctioid **2a** plate to mid-right; × 5000. 7–8, specimen lost. 7, internal view of isolated epitheca, showing reflected tabulation; note apical pore to right centre and first apical plate extending from this at 45°; × 2700. 8, detail showing apical pore and plate **3′**; note overlapping plates have a groove parallel to the plate margin, the suture between overlapping and overlapped plate margins is ragged and bisects trichocyst pores; × 7000.

Figs 9–12. *Lithoperidinium* sp. sample COC4; Coconut Grove, near Springfield, Barbados; Oceanic Formation, Eocene; SM X.24553. 9, apical view showing prominent parasutural ridges bounding plates **2′**–**4′**; × 1600. 10, ventral view showing prominent flagellar pore and narrow, parallel-sided nature of the parasulcus; × 1700. 11, apico-ventral view showing very narrow first apical paraplate leading to apical pore; microperforated region on paraplate **1″** is an adherent diatom fragment; × 1700. 12, oblique, apical-right lateral view; note long, narrow **6″** and narrow, asymmetrical **5″**; × 1700.

PLATE 2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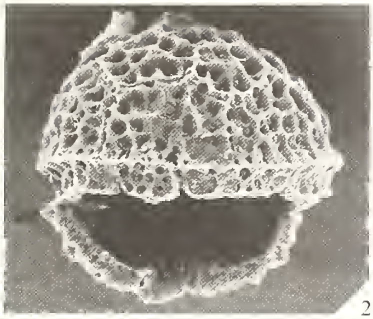
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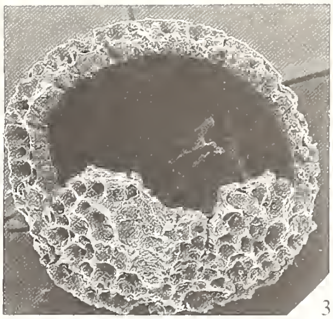
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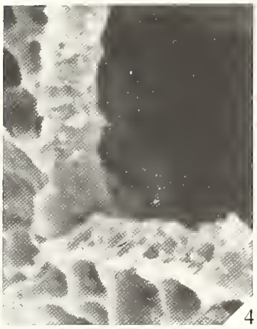
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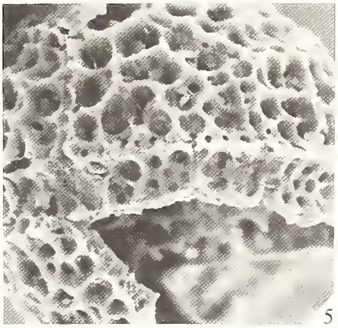
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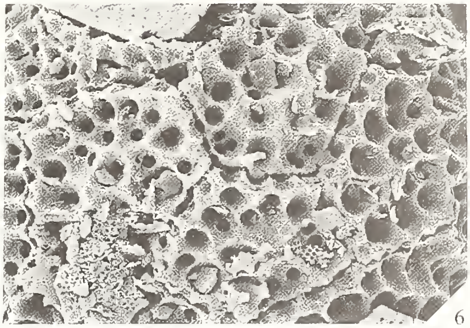
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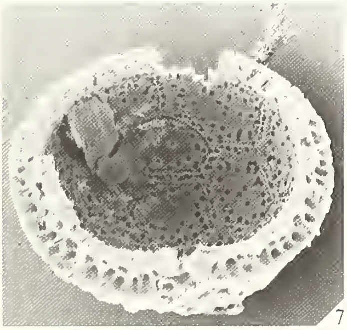
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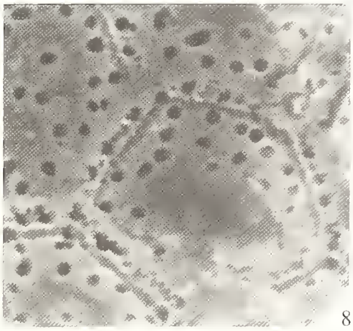
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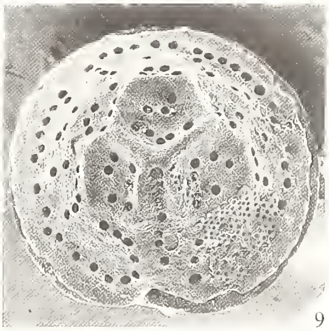
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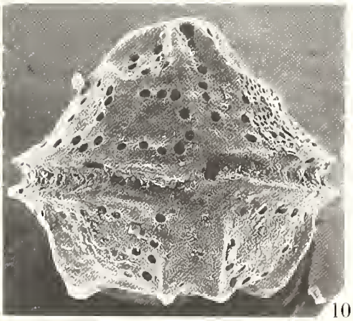
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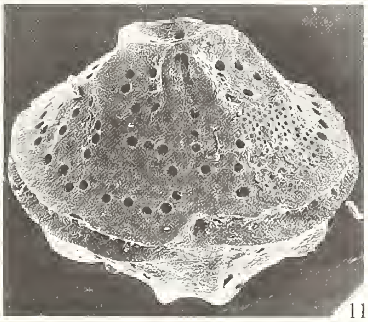
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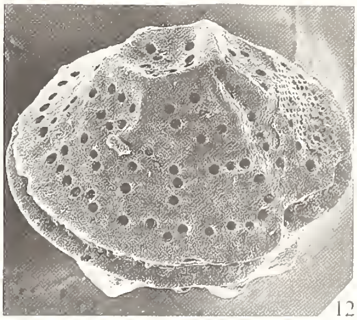
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HARDING and LEWIS, *Peridinites*, *Lithoperidinium*

Peridinites as being siliceous organisms, this primary mineralization leading to the fossilization of the motile thecate stage.

SYSTEMATIC PALAEONTOLOGY

Discussion. Re-examination of the type material of *Peridinites* Lefèvre, 1933*a* and *Lithoperidinium* Deflandre, 1933 (by ICH), has indicated the dissimilarity between the two genera. Whereas *Peridinites* is thin-walled, and commonly incomplete and fragmentary in its preservation, specimens of *Lithoperidinium* are much more robust, possess a wall at least three times the thickness of that of *Peridinites*, and yet are of approximately the same dimensions. Optically, the sutural features of *Lithoperidinium* appear non-functional. For these reasons, we do not follow the synonymy of Deflandre (1945) and Norris and Sarjeant (1965), who designated *Lithoperidinium* Deflandre, 1933 as a synonym of *Peridinites* Lefèvre, 1933*a*. Neither do we accept the use of *Lithoperidinium* as the senior synonym (Fensome *et al.* 1993; Lentin and Williams 1993) but retain both genera. *Peridinites* is a siliceous dinoflagellate fossil, here identified as the thecal stage in the life cycle, rather than a hypnozygotic cyst; we herein emend this genus. *Lithoperidinium* is interpreted as being the fossilized cyst stage of the life cycle and is also emended. We follow the classification scheme of Fensome *et al.* (1993), but note that their description of Lithoperidinioideae mentions only the cyst stage of the life cycle. We expand this to incorporate the thecate stage of the life cycle and hence include *Peridinites* in this subfamily. The discrimination of *Jusella* Vozzhennikova, 1963 from *Lithoperidinium* Deflandre, 1933 is regarded as being based on morphological features not of generic rank, making *Jusella* a later synonym of *Lithoperidinium*.

Division DINOFLAGELLATA (Bütschli, 1885) Fensome *et al.*, 1993
Subdivision DINOKARYOTA Fensome *et al.*, 1993
Class DINOPHYCEAE Pascher, 1914
Order PERIDINIALES Haeckel, 1894
Family PERIDINIACEAE Ehrenberg, 1832
Subfamily LITHOPERIDINIOIDEAE (Deflandre, 1945) Fensome *et al.*, 1993
Genus PERIDINITES Lefèvre, 1933*a* emend. nov.

Type species. *Peridinites parvulus* Lefèvre, 1933*a*.

Emended diagnosis. Subspherical to pyriform dinoflagellate thecal fossils. Epitheca and hypotheca of approximately equal dimensions, separated by a prominently indented, descending cingulum. Sulcus confined to hypotheca in the form of a parallel-sided longitudinal furrow. Theca composed of heavily sculptured plates completely perforated by many trichocyst pores and separated one from another by functional sutures. Tabulation: **Po, 4′, 3a, 7″, ?6c, 5‴, 2⁗, ?s**. Hypothecal ecdysal opening comprising at least **2‴–4‴**.

Peridinites piriformis Lefèvre, 1933*a*

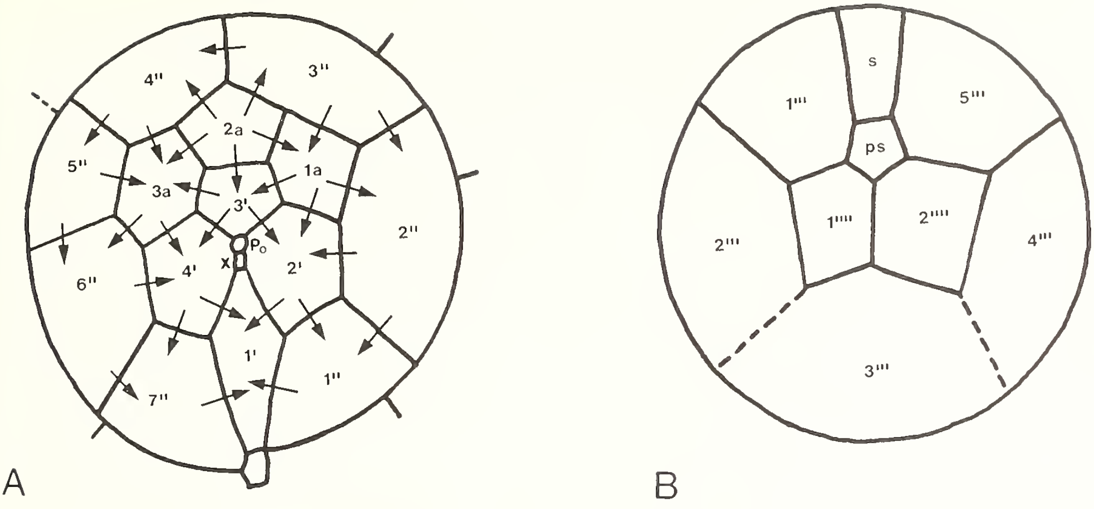
Plate 1, figures 1–7, 9–12; Text-figure 4

v*1933*a* *Peridinites piriformis* Lefèvre, p. 417.
v*1933*b* *Peridinites piriformis* Lefèvre; Lefèvre, p. 225, figs 17–18.

Emended description

Shape. Pyriform, with a short, pronounced apical horn (Pl. 1, figs 1, 6). There is no indication of primary dorsoventral compression. Epitheca slightly larger than hypotheca.

Wall structure. The single wall is up to 2 μm in thickness. The sculpture takes the form of an irregular reticulum consisting of laevigate muri rising to a sharp, knife-edge culmination. The lumina (1–3 μm in diameter) are fairly deeply excavated and may contain one or more pores at the base. These trichocyst pores (0·5 μm in diameter) fully penetrate the thecal wall (Pl. 1, figs. 5, 7). The majority of trichocyst pores are regularly lined



TEXT-FIG. 4. A, epithecal tabulation and plate overlap patterns (as far as have been discerned) of *Peridinites piriformis*. Tabulation and plate overlap, as far as can be discerned is the same for *P. sphaericus*. B, hypothecal tabulation of *P. piriformis*. Tabulation, as far as can be discerned, is the same for *P. sphaericus*.

up along the plate sutures, although a few are irregularly scattered in intratabular positions (Pl. 1, fig. 7). The ovate apical pore (1·5 × 2·0 μm) is surrounded by a raised collar and is of the typical peridinioid form (Pl. 1, fig. 12).

Cingulum. Indented and slightly offset by about one cingular width. Three cingular sutures have been found adjacent to **1″**, **2″**, **3″**. It has not been possible to analyse the right-hand side of the specimens. Referring to the discussion under *P. sphaericus*, it seems likely that this species has a full complement of six cingular plates.

Sulcus. Parallel-sided, slightly depressed but tabulation poorly defined. A single ovate flagellar pore (3 μm in diameter) is located where the cingulum joins with the sulcus.

Tabulation. Externally, the overlapping margins are bounded by sharp-edged ridges, the overlapped margin showing a linear concentration of trichocyst pores. Internally, the overlapping plates bear a linear groove parallel to the plate margin, the suture between plates being a fissure close to the line of trichocyst pores. The keystone plates are **2a** and **3‴**. The epithecal tabulation is characteristically cinctioid – **Po, x, 4′, 3a, 7″** (Pl. 1, fig. 1; Text-fig. 4A). The apical pore plate (**Po**) is circular and is joined to the wide first apical plate by a short canal plate (**x**) (Pl. 1, figs 6–7). The first and second intercalaries are pentagonal with a hexagonal third intercalary plate. Ventral epithecal tabulation is ortho. Hypothecal tabulation (**5‴**, **2⁗**) is known in more detail than that of *P. sphaericus*, as one specimen has been observed with antapical plates in place (Pl. 1, fig. 4; Text-fig. 4B). Antapical plates are relatively small in comparison to the post-cingular series. The ecdysal opening is formed by the loss of **2‴–4‴**.

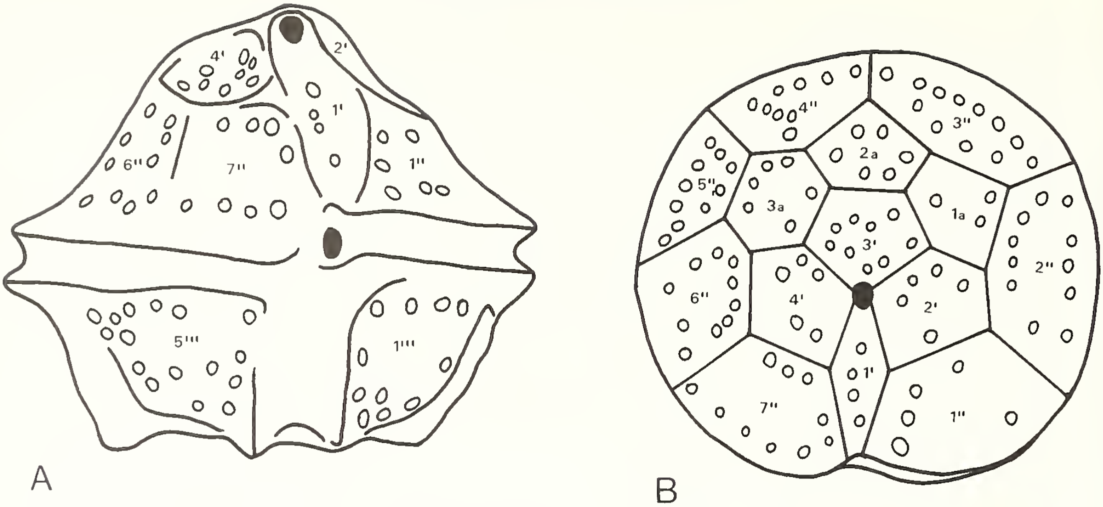
Dimensions. Equatorial diameter (26) 27 (28) μm (6 specimens measured).

Remarks. Examination of the type specimens in Paris, and the collection and study of new topotype material from Barbados, has allowed a precise redescription of the species. The specimens here assigned to *P. piriformis* are directly comparable to the size range given by Lefèvre (1933*b*). The thecal nature of the specimens is emphasized.

Peridinites sphaericus Lefèvre, 1933*a*

Plate 2, figures 1–8

v*1933*a* *Peridinites sphaericus* Lefèvre, pp. 416–417.



TEXT-FIG. 5. A, ventral tabulation of *Lithoperidinium* sp. B, epicystal tabulation of *Lithoperidinium* sp.

v*1933_b_	*Peridinites sphaericus* Lefèvre, pp. 223–224, figs 13–14.
v*1933_b_	*Peridinites sphaericus* var. *minor* Lefèvre, p. 224, text-fig. 24.
1973	*Peridinites sphaericus* ssp. *minor* Lentin and Williams, p. 111.

Emended description

Shape. Ambitus subspherical (Pl. 2, fig. 2). No evidence of primary dorso-ventral compression. Epitheca slightly larger than hypotheca, and produced into a very short, blunt apical horn.

Wall structure. The single wall layer is up to 2 μm thick (Pl. 2, fig. 4). The wall is fragile and prone to fragmentation along the plate sutures. Sculpture consists of an irregular raised reticulum consisting of mural ridges reminiscent of modern gonyaulacoid sculptural features. Luminal diameters range from 0·75 μm to 4 μm, with an average around 1·5 μm diameter. Muri width ranges from 0·30–0·75 μm. Each lumina shows a pronounced concavity, and the majority possess a basal pore-like perforation, which fully penetrates the wall layer. These perforations, interpreted as trichocyst pores, are distributed fairly evenly over the plates, although linear concentrations are found along the adcingular sutures (Pl. 2, figs 5, 8) in a similar manner to those of modern thecae. At the apex of the horn is a circular apical pore surrounded by a low collar which is of the typical peridinioid form (Pl. 2, fig. 6).

Cingulum. This takes the form of a pronounced subequatorial indentation which is very slightly offset by about one half of a cingular width. Four cingular sutures have been found adjacent to plates **1″**, **2″**, **3″** and **7″**. However, we have not been able to check to our satisfaction the areas lying adjacent to **4″–6″**. Lefèvre (1933*a*, 1933*b*) does not figure or list the numbers of cingular plates, but in one diagram of *Peridinites barbadensis* a cingular suture adjacent to the **5″** plate is shown. This implies a probable complement of six cingular plates.

Sulcus. Parallel-sided and poorly defined.

Tabulation. Sutures appear fully functional, being visible on both internal and external surfaces (Pl. 2, figs 1–8). Externally, plate overlap direction is indicated by a high scalloped plate margin on the overlapping plate, the underlapped margin being of much lower relief (Pl. 2, fig. 6). Internally, the overlapping plates bear a linear groove parallel to the plate margin, the suture between plates being a fissure close to the line of trichocyst pores. The second anterior intercalary is the epithecal keystone plate overlapping all of its neighbours (Pl. 2, figs 2, 6). Epithecal tabulation is characteristically cinctioid—**Po, x, 4′, 3a, 7″**. The apical pore plate (**Po**) is circular and is joined to the narrow first apical plate by a short canal plate (**x**). The first and second intercalaries are pentagonal with a hexagonal third intercalary plate. Ventral epithecal tabulation is ortho. The hypothecal tabulation is **5‴**, **2⁗**.

Ecdysal opening. The formation of an ecdysal opening appears to involve plates $2'''$–$4'''$, although in most instances $1''''$ and $2''''$ are also lost (Pl. 2, fig. 3). This pattern is lost on some specimens as the removal of these plates leaves the remaining hypothecal plates unsupported leading to complete hypothecal fragmentation in many specimens (Pl. 2, fig. 7).

Dimensions. Equatorial diameter (29) 31·2 (35) μm (6 specimens measured).

Remarks. Examination of the type specimens in Paris, and the collection and study of new topotype material from Barbados has allowed a precise redescription of the species. Lefèvre (1933*b*) originally distinguished specimens of *P. sphaericus* and *P. sphaericus minor* purely on the basis of size, the former varying from 32–40 μm, the latter from 25–30 μm. Such size variation is commonly found amongst thecal dinoflagellates and is not deemed to be worthy of subspecific importance. The thecal nature of the specimens is emphasized.

Genus LITHOPERIDINIUM Deflandre, 1933

1963 *Jusella* Vozzhennikova, p. 183

Type species. Lithoperidinium oamaruense Deflandre, 1933.

Remarks. Lithoperidinium is reinstated as a genus of siliceous dinoflagellate hypnozygotic *cysts*. Vozzhennikova (1967) retained both *Peridinites* and *Lithoperidinium*, and furthermore introduced the new siliceous genus, *Jusella*. Following Vozzhennikova (1967) and Deflandre (1940), and using the evidence presented above, we retain both *Peridinites* and *Lithoperidinium* as separate genera; the former as a genus of thecal fossils, and the latter as a genus of cyst fossils.

The taxonomic position of *Jusella* Vozzhennikova, 1963 is less clear. *Jusella* was differentiated from the other two genera by Vozzhennikova (1967) by having larger pores, coarser sculpture and a different tabulation to the hypotheca (*sic*), showing an intermediate plate between the longitudinal furrow and the antapical plates. We do not believe that either pore size or expression of sculptural features are valid criteria on which to separate these genera. Wide variations in sculpture are to be found in single species of extant dinoflagellates (Dodge 1989; Lewis and Burton 1988). The presence of an 'intermediate plate', which would now be known as a posterior sulcal plate, is also a dubious taxonomic criterion, given the variability in the expression of tabulation reported for some dinocyst genera. Present evidence indicates that *Jusella* should be more properly viewed as a synonym of *Lithoperidinium*.

Dale (1983, fig. 26) illustrated a siliceous dinoflagellate specimen from the Eocene of the Norwegian Sea, which he identified as *Peridinites globosus*. By comparison with specimens isolated in the present study, the specimen illustrated by Dale would be more properly allocated to *Lithoperidinium*.

Lithoperidinium sp.

Plate 2, figures 9–12; Text-figure 5

Description

Shape. A squat, prolate spheroidal cyst with a low conical epicyst and flattened hypocyst. Dorso-ventral ambitus angular, with rectangular hypocyst outline. Equatorial ambitus subspherical, indicating absence of primary dorso-ventral compression (Pl. 2, fig. 9). Epicyst slightly longer than hypocyst, and produced into a low, blunt apical horn (Pl. 2, fig. 10).

Wall structure. Laevigate wall up to 5 μm in thickness (punctate area on Pl. 2, fig. 11 is an adpressed diatom fragment). Large pores (up to 2 μm in diameter) are the most evident feature on the external surface of the cyst being distributed in a penitabular manner. Paratabulation is indicated by low ridges on the majority of the precingular paraplates, but on the remaining apical and hypocystal paraplate series, the ridges are more pronounced and may reach 4 μm in basal width. The position of the apical pore is marked by the meeting of the gentle ridges which surround the paraplates.

Paracingulum. Cyst is divided equatorially by a strongly indented paracingulum, which is offset by one paracingulum width.

Parasulcus. The parasulcus is little more than a shallow groove bordered by parallel ridges; detailed paratabulation is not expressed.

Paratabulation. As far as has been determined the paratabulation is cinctioid (Text-fig. 5). Parasutures on the precingular paraplates are not clearly defined and are marked by low ridges and penitabular pores. The remaining parasutures are better defined by low, broad ridges. Ventral epicystal paratabulation is ortho-style. The first apical plate is narrow.

Dimensions. 49 μm diameter (single specimen measured).

Remarks. This morphotype is clearly of a different structural nature from that of the specimens here assigned to the genus *Peridinites*. The most important morphological feature which points to this form being a dinoflagellate *cyst* rather than a fossilized *theca* is the non-functional nature of the junctions between paraplates. The size of this specimen (and its overall morphology when observed in the light microscope), is compatible with that given by Vozzhennikova (1967) for *Jusella* (*sic*) *denticulatum*.

CONCLUSIONS

Our initial belief was that the lack of reports of *Peridinites* was due to the biasing of sample residues by differential sieving by radiolarian workers, who routinely examine size fractions greater than 63 μm. The greatest concentration of *Peridinites* in samples so far examined, yielded a ratio of *Peridinites* specimens to other siliceous microfossils of the order of 1:100000. This extreme rarity appears to negate any possibility of the genus being used as a routine biostratigraphical index fossil, but examination of the temporally more extensive Bath Cliffs section on Barbados (Eocene to Miocene in age) may yield data indicating greater abundance in certain time intervals.

Detailed analysis of the tabulation patterns of the species of *Peridinites* corroborate the observation by Masure (1990), that the siliceous peridinioids may have evolved from heterocapsiform ancestors in which two dorsal apical plates may have fused into a single third apical plate seen in peridinioid dinoflagellates.

A detailed light and electron microscopic elucidation of the morphology of *Peridinites*, based on type and new topotype material, indicates that the genus represents not only the first reported unequivocal dinoflagellate thecal fossils, but also the only dinoflagellates known to be capable of secreting primarily siliceous thecal plates. The discovery that *Peridinites* represents a thecal fossil has made the postulation of methods of silica secretion in the fossils difficult, due to the lack of any modern analogues amongst living thecate dinoflagellates.

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A NEW ORDOVICIAN ARTHROPOD, *SOOMASPIS*, AND THE AGNOSTID PROBLEM

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ABSTRACT. A new uncalcified arthropod, *Soomaspis*, is described from the latest Ordovician Soom Shale of South Africa. It is included with other primitive and uncalcified trilobites in the family Naraoiidae, the composition and evolution of which are re-evaluated. Naraoiids are considered to have arisen by the heterochronic process of hypermorphosis, whereas Agnostida, to which they bear a superficial resemblance, are progenetic. The place of *Soomaspis* and naraoiids within the trilobite-like arthropods is analysed cladistically; they comprise a sister group of the rest of the clade. The problem of classifying Agnostida is discussed in this context. Their relationships within, or outside Trilobita depend upon the methods of character analysis, and the emphasis placed on particular characters. In the analysis presented here, Agnostina comprise the sister group of Eodiscina. The inclusion of all these groups within the Trilobita is favoured.

SINCE the first description of Lower Palaeozoic fossils from the Table Mountain Group of South Africa (Cocks *et al.* 1970), continued research has elucidated the distribution and age of this unique fauna. The fossiliferous beds are confined to the Cedarberg Formation, a laterally persistent argillaceous unit (*c.* 120 m) among predominantly arenaceous rocks (*c.* 3000 m), which build up an impressive sequence of rugged mountain ranges in the southwestern Cape Province. Good exposures of the Cedarberg Formation are rare because of its recessive nature, and are seldom easily accessible. Consequently, fifteen years passed before Moore and Marchant (1981) discovered in the basal Soom Member the well-preserved trilobites described by Cocks and Fortey (1986) as *Mucronaspis*. From the trilobite and brachiopod faunas, they concluded that the age of the Soom as well as the overlying Disa Member was latest Ordovician, rather than early Silurian (Llandovery) as had been suggested by some previous authors.

Further investigation of the Soom Member resulted in the discovery of a new fauna more than 100 km north of the previous fossil sites. This fauna includes exceptionally well-preserved, giant conodont apparatuses (Theron *et al.* 1990; Aldridge and Theron 1993) sometimes preserving soft tissues of the animals, as well as eurypterids, brachiopods and orthocone nautiloids. The same fauna includes an unusual arthropod, which is the subject of this paper.

South Africa lay at high palaeolatitudes in the late Ordovician (Scotese and McKerrow 1990). The Soom Shale conformably overlies and sometimes partially interfingers with tillites of the Pakhuis Formation. It is therefore a rare example of a Palaeozoic glacio-marine depositional environment, the Soom Shale representing the outwash and fine silt fraction from the retreating ice sheet, while the fauna is indicative of open marine conditions.

The new arthropod, *Soomaspis*, is a rare fossil. It is of particular importance, however, because it is one of a group of trilobite-like animals (naraoiids) which have been claimed as related to the trilobite suborder Agnostina (which will be referred to, informally, as 'agnostids'). Some recent authors (e.g. Shergold 1991) have claimed that agnostids are not closely related to other trilobites. *Soomaspis* provides an opportunity to look again at the evidence for agnostid relationships, and to assess how naraoiids fit into the stem lineage of the Trilobita.

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COMPOSITION OF NARAOIIDAE

Naraoia was originally described from the celebrated Middle Cambrian Burgess Shale of British Columbia by Walcott (1912). The type species, *N. compacta*, and a second one, *N. spinifera* Walcott, 1931, were exhaustively revised by Whittington (1977). Because the type species has limbs preserved on many specimens, a good deal is known about its appendages, which led Whittington to make a comparison with the Trilobita, to which clade *Naraoia* was assigned as an unmineralized member. Raymond (1920) had proposed an Order Nektaspida for its reception.

Naraoia has turned out to be quite widespread. Robison (1984) reported *N. compacta* from the upper Lower to Middle Cambrian of Idaho and Utah. Zhang and Hou (1985) described new and well-preserved *Naraoia* species from Chengjiang, eastern Yunnan, China, from the Lower Cambrian. This last occurrence is particularly important because it proves that the differentiation of naraoiids from other arthropods has happened already as part of the so-called Cambrian 'explosion'. Stratigraphical evidence is therefore irrelevant for the resolution of the relationships of *Naraoia*, which must be determined by a consideration of comparative morphology using cladistic methods (Briggs *et al.* 1992; Fortey and Owens, 1990).

Here we include several more genera besides *Naraoia* in the family Naraoiidae. These are: *Liwia* Dzik and Lendzion, 1988; *Tarricoia* Hammann *et al.* 1990; *Soomaspis* gen. nov.; and *Maritimella* Repina and Okuneva, 1969. The least fully known of these are *Liwia* and *Maritimella*, but knowledge of the dorsal morphology of the other two is sufficient to provide a good comparison with *Naraoia*, from which they differ primarily in having freely articulated thoracic segments.

The Naraoiidae have the following characters, most of which are regarded as autapomorphies.

1. The cephalic shield is transversely oval or semicircular, and virtually without dorsal features; there are no eyes.

2. The pygidium exceeds the cephalic shield in length (sag.). This is an unusual feature in arthropods; it is only otherwise known on some undoubtedly advanced trilobites, such as Devonian Scutelluidae (e.g. Šnajdr 1981). For this reason, we regard it is a good character of phylogenetic significance. As discussed below, the large pygidium is likely to have been the result of the heterochronic process known as hypermorphosis. Hammann *et al.* (1990, fig. 5) reconstructed *Tarricoia* as having the pygidium only slightly exceeding the cephalic shield in length. Specimens from the type locality of *T. arruseusis* are all distorted in various ways and accurate assessment of proportions is accordingly difficult. A visit to the type locality by the first author and Dr L. R. M. Cocks yielded the specimen shown on Plate 1, figure 1, which apparently shows little distortion. Its pygidium is relatively longer than that in the reconstruction of Hammann *et al.*, and more like that of other naraoiids. We have introduced this modification to the proportions of *Tarricoia* in the discussions used in this paper. The character is least developed on the new genus described below.

3. Naraoiids are medium sized trilobites, commonly 20–30 mm in length; Chinese species include larger individuals. They are several times the size of the average agnostid (below).

4. There are few to no thoracic segments. The primitive state in Arthropoda is likely to have included a large number of freely articulating post-cephalic segments (Manton 1977; Briggs *et al.* 1993), and loss of such segments is generally considered to be an advanced character. On the other hand, we would attribute little systematic importance to the presence of three or four free thoracic segments in *Soomaspis*, *Liwia* and *Tarricoia*, as opposed to none in *Naraoia*. The retention of a few thoracic segments is probably a pleisomorphic character, which is not an important consideration in the placement of the group as a whole.

There are other naraoiid characters which are probably plesiomorphic. These include possession of a single pair of filiform antennae (known in *Naraoia* and *Liwia*), and the generally trilobitomorph limb structure (*Naraoia*, see Whittington 1977). Genal spines are known in *Naraoia spinosa* Zhang and Zhou and, probably, in *N. spinifer* Walcott also. Genal spines are a general trilobite character, and their loss in other naraoiids is a derived character, but it is not a general feature of the group.

SYSTEMATIC PALAEONTOLOGY

Class TRILOBITA Walch, 1771
Order NEKTASPIDA Raymond, 1920
Family NARAOIIDAE Walcott, 1912
Subfamily LIWIINAE Dzik and Lenzion, 1988
Genus SOOMASPIS gen. nov.

Type species. Soomaspis splendida sp. nov.

Diagnosis. The diagnosis follows that of the type and only species, given below.

Soomaspis splendida sp. nov.

Plate 1, figures 2–4; Text-figure 1A–C

Type locality. Soom Shale, Keurbos Farm near Clanwilliam, Cape Province, South Africa (full locality details given in Theron *et al.*, 1990).

Holotype. Dorsal exoskeleton, showing rostral plate, Geological Survey of South Africa collection, specimen number C453.

Paratypes. Two other complete dorsal exoskeletons C405, C451; three fragmentary shields, C313, C374, C696.

Diagnosis. Naraoiid having pygidium with five segments defined by interpleural furrows. Thorax with three thoracic segments. Surface sculpture of dense pitting.

Description. The largest cephalic shield has a width of just under 20 millimetres, which suggests that the entire animal must have attained a length of at least 30 mm. Because the cuticle was unmineralized, little is preserved of the original relief. The entire exoskeleton shows signs of crushing, especially on the pygidium, and differential compaction may account for differences between the holotype and the several paratypes, with regard to such features as the clarity of pygidial segmentation and convexity of the sagittal area. Whittington (1977) inferred moderate convexity on *Naraoia compacta*, and *Soomaspis* was probably similar. However, the crushing renders measurements of proportions somewhat approximate. Cracks on the pygidium of the holotype run close to the pygidial axis, and on the exsagittal right- and left-hand side of the cephalic shield (Text-fig. 1A), which is consistent with crushing a somewhat convex median lobe. For example, the trilobite *Bienvillia* developed cracks in a comparable position when preserved in flattened mode (Fortey 1974, pl. 22, figs 9, 11).

The whole exoskeleton is about two-thirds as wide as long. Maximum width is across the cephalic shield, which is about 1·3 to 1·4 times the width of the pygidium. The pygidium slightly exceeds the cephalic shield in length, but in view of the flattening it is difficult to be precise by how much. The cephalic shield on the paratype (Text-fig. 1C) appears to preserve its anterior margin and is more than twice the sagittal length of the thorax behind it. The cephalic shield is subsemicircular to elliptical, and virtually featureless. The holotype (Text-fig. 1A), and right hand side of the specimen on Text-figure 2B, show flattened areas which are regarded as narrow posterior borders, which curve gently forwards laterally.

The holotype uniquely shows an area of cuticle lying anterior to the cephalic margin. This is not easy to interpret. To either side of, and beneath the genal regions of the same specimen there are indications of a comparatively wide doublure. This median region seems likely to represent the median part of the doublure. In this case, the lateral edges of this piece of cuticle probably represent the connective sutures; this is what would be termed the rostral plate in other trilobites. This interpretation would suggest that the holotype is a specimen which has moulted, in the course of which the cephalic shield was pushed a little backwards and the mid part of the doublure displaced forwards in the same action. If correct, this proves the cephalic doublure to be comparatively wide (sag.), as it is in *Tarricoia*. The specimen in Text-figure 1B shows a wide and ill-defined front to the cephalic shield which may be the result of crushing a similarly moulted individual.

The thorax apparently comprises three segments. It is necessary to be a little cautious about this, because the allied genera *Tarricoia* and *Liwia* both have four segments. Hammann *et al.* (1990) showed that the anterior segment in *Tarricoia* is often covered and concealed by the cephalic shield. However, the incomplete specimen on Text-figure 1c, which has the cephalic shield tipped slightly to one side, also shows three thoracic segments and no trace of a fourth. On the other hand, the specimen on Text-figure 1b apparently shows only two thoracic segments, as (undoubtedly) does the isolated thorax and pygidium (Pl. 1, fig. 3). The most likely interpretation is that there *are* three thoracic segments but that, as in *Tarricoia* (Hammann *et al.* 1990), the anterior segment is often concealed beneath the cephalic shield. It does not seem probable that there are two species, characterized by two or three segments respectively, because the other characters are so similar in all our material.

Each segment is a narrow, band-like strip of exoskeleton with poor indication of the axis. The specimen on Plate 1, figure 2 shows evidence of division into a broad axial region and narrow pleural regions. Pleural tips are truncate. The anterior segment on the specimen figured on Plate 1, figure 3 clearly shows the articulating half ring across the mid part of the axis. It is short (sag.), occupying about a third of the width of the axial ring. Axial rings provide good evidence for free articulation of the thoracic segments, but this movement is likely to have been limited in the dorsoventral plane as shown by the short half rings. Details of the articulation are not visible, but there is no evidence of strong ball-and-socket joints, as in advanced Trilobita. Plate 1, figure 2 shows extremely thin, depressed bands on the anterolateral margins of the segments, which fitted against the pleurae of the segment in front.

The pygidium is just wider than long. There is a striking difference between the two best specimens (Pl. 1, figs 2–3). The larger has a prominent elevated median band which is not evident on the smaller. The latter specimen shows additional details on the axial region. However, the crack running sagittally on this specimen may have served to reduce the prominence of any ridge. A median ridge is present also on other complete specimens of *Soomaspis*, and also the pygidium of *Tarricoia*. It is unlikely that the median ridge is the trace of the soft gut impressed on the dorsal surface. If it were filled with sediment, one might expect to see signs of the cuticle draping around such a structure as it decayed, for which there is no evidence. It is considered more likely to have been an original structure, as in *Tarricoia*, possibly exaggerated by flattening. Pleural fields include five segments bounded by distinct furrows which are present on the outer parts only of the pleural fields. The posterior ends of the interpleural furrows curve backwards into spine-like terminations, but these do not apparently project beyond the pygidial margin. Where the furrows stop adaxially, this delimits the axial region, which therefore takes up more than one-third of the pygidial width anteriorly. Such an interpretation is supported by the presence of muscle scars on the outer edge of this region (Pl. 1, fig. 2), shown by one specimen. Three such pairs are clearly shown, each lying close to a segmental boundary, and transversely elliptical in outline. Presumably similar muscle attachment areas were related to posterior segments also, but their trace is obscure. The specimen on Plate 1, figure 3 (left hand side) in particular shows an anterior pygidial border, which appears to extend farther adaxially than the inferred width of the axis. The same specimen shows the narrow doublure (right hand side), which narrows farther backwards. The dorsal surface of the pygidium certainly, and the mid-part of cephalon probably, is covered with rather coarse pits (Pl. 1, fig. 4).

Discussion. The type and only known species of *Soomaspis* can be compared with those nektaspids with thoracic segments. The closest stratigraphically is *Tarricoia arrusensis* Hammann *et al.*, 1990, from the Ordovician 'Puddinga' sequence of Sardinia. *Tarricoia* has four thoracic segments, and the pygidium is entirely without dorsal segmentation (Pl. 1, fig. 1). *Tegopelte gigas* Simonetta and Della Cave, 1975, from the Middle Cambrian Burgess Shale has three thoracic divisions according to Whittington (1985). This is a very large arthropod, of which the dorsal side is poorly known. Whittington showed that the three thoracic divisions, which are unusually long (sag.), included several limb pairs per division, which is unique. *Tegopelte* is also thought to have had eyes inserted

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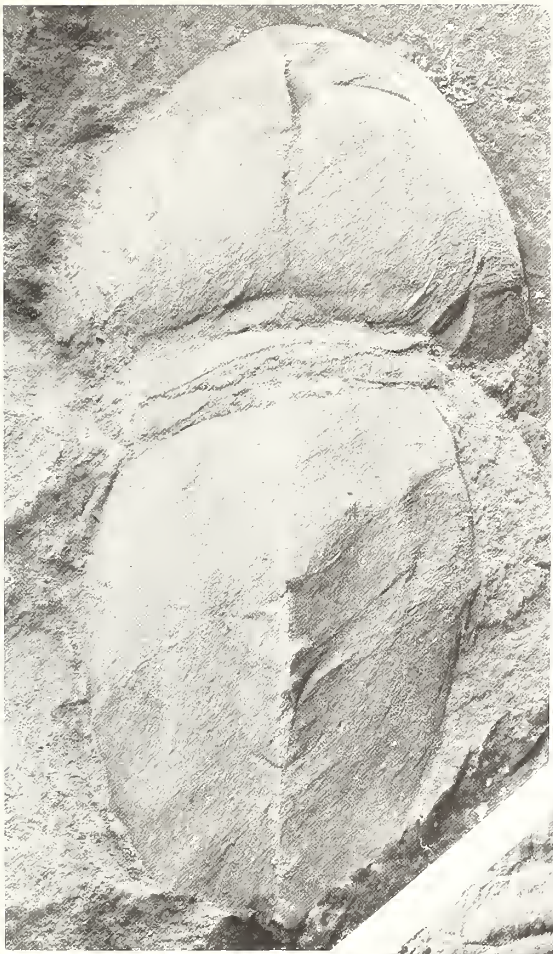
EXPLANATION OF PLATE 1

Fig. 1. *Tarricoia arrusensis* Hammann *et al.* Natural History Museum, It 21084; type locality, near Fluminimaggiori, southwest Sardinia; 'Puddinga' Formation (Ordovician); ×4.

Figs 2–4. *Soomaspis splendida* gen. et sp. nov. Paratypes; Keurbos farm, near Clanwilliam, South Africa; Soom Shale (Ordovician). 2, Geological Survey of South Africa, specimen C405; latex cast from external mould of entire dorsal shield showing pygidial musculature; × 7.5. 3–4, Geological Survey of South Africa, specimen C313; pygidium and two thoracic segments; 3, internal mould showing doublure; ×8; 4, detail of external mould showing anterior border furrow; ×10.

PLATE 1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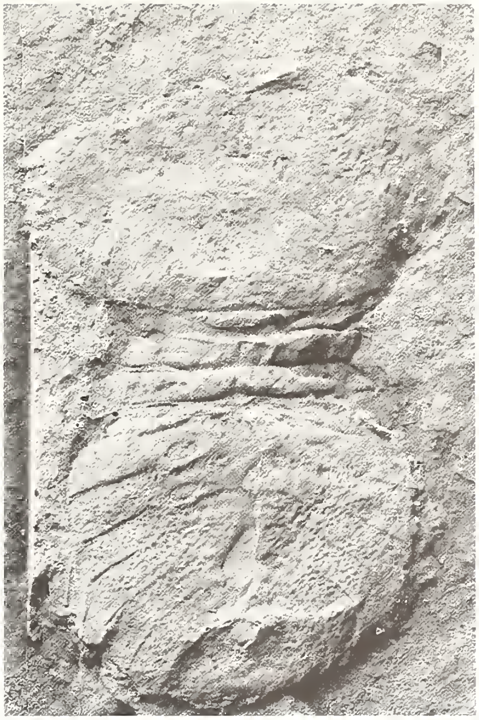
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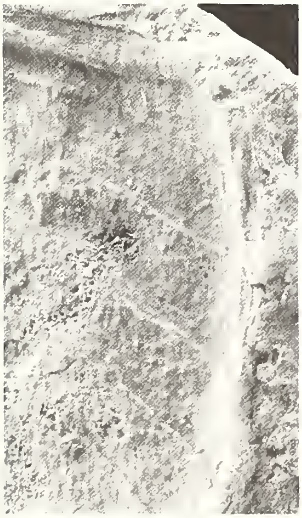
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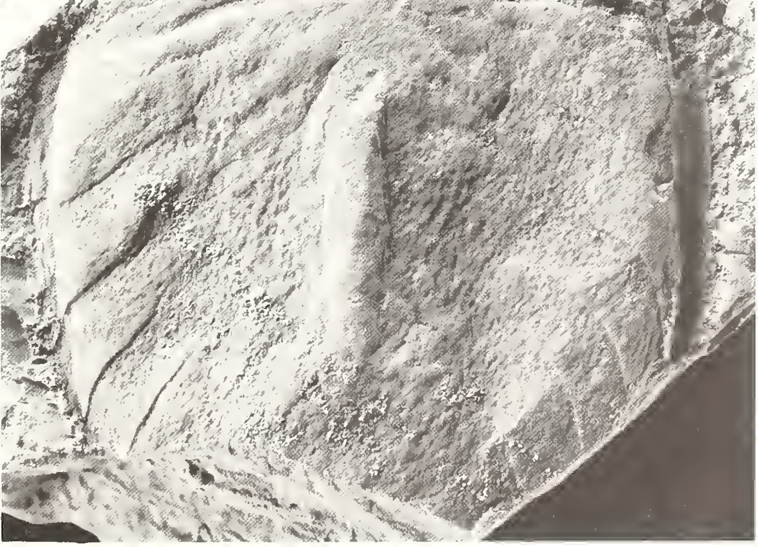
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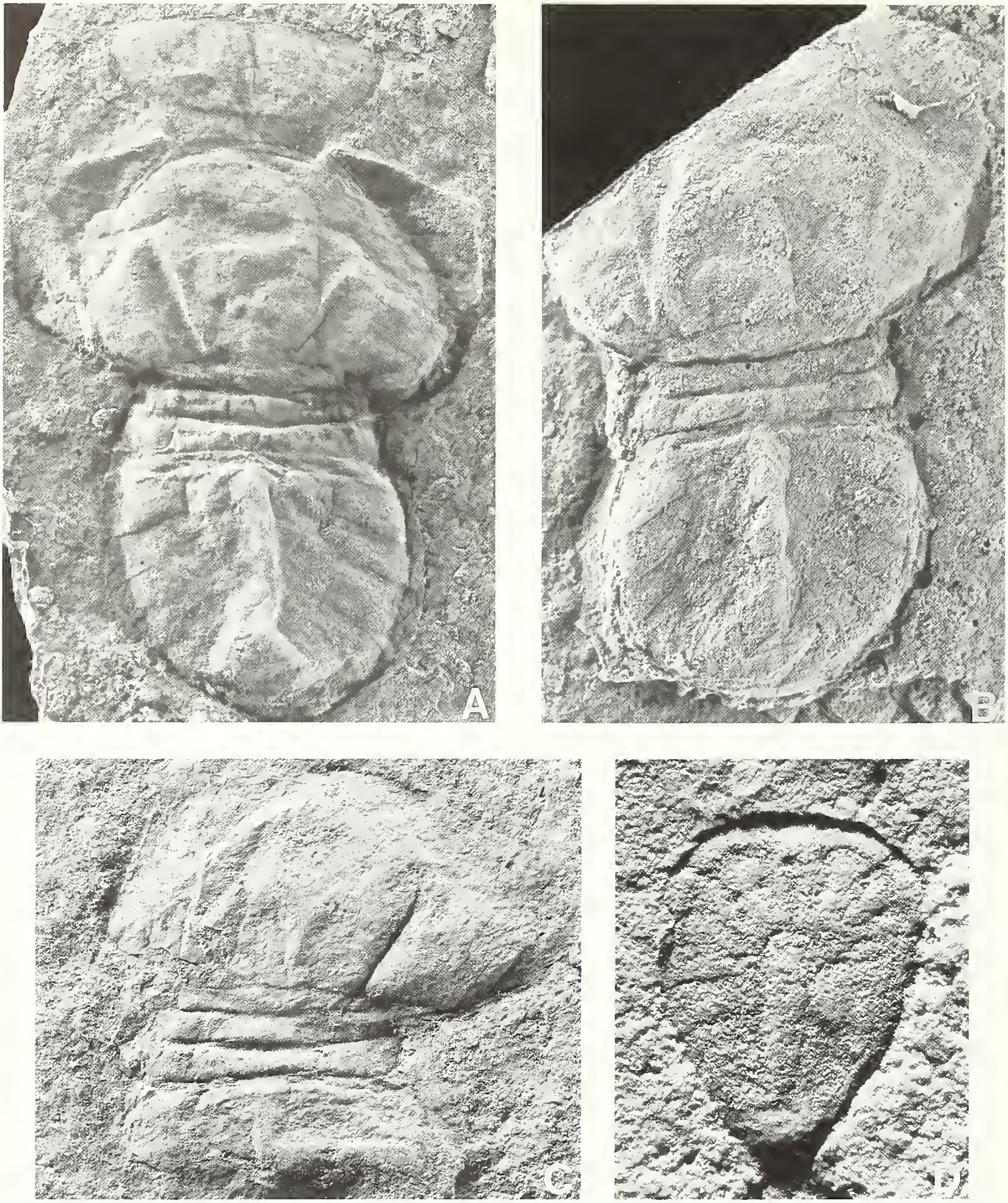
FORTEY and THERON, *Tarricoia*, *Soomaspis*



TEXT-FIG. 1. A–C, *Soomaspis splendida* gen. et sp. nov.; specimens stored at the Geological Survey of South Africa; Keurbos farm, near Clanwilliam, South Africa; Soom Shale (Ordovician). A, C453; latex cast of holotype, with doublure; × 5. B, C451; latex cast of paratype; poor anterior definition of cephalic shield may be due to conflation with doublure; × 5. C, C374; internal mould of incomplete larger specimen showing three thoracic segments; × 4. D, giant protaspis cautiously attributed to *Naraoia* by Hou *et al.* (1991); Nanjing Institute of Geology and Palaeontology, specimen 115282 (photograph kindly supplied by Dr J. Bergström); Chenjiang fauna, China; Lower Cambrian; × 16.

on the cephalic shield. We agree with Whittington's assessment that its trilobite status is uncertain. *Maritimella* Repina and Okuneva (Middle-Upper Cambrian, Far-eastern Russia) presents another problem, in that it looks, superficially at least, much like *Naraoia*, but is described as having dorsal eyes and 'convexities' on the 'opisthosoma' (? = pygidium). The question is, perhaps, its distinction or not from *Naraoia*, and it will not be discussed further here.

The genus *Liwia* was described from basal Cambrian claystones from Poland (see Dzik and Lendzion 1988). Like *Tegopelte*, it is imperfectly known, but it does provide the closest comparison with *Soomaspis*. The presence of antennae on *Liwia* is of no significance, because they are symplesiomorphic for Trilobita (and indeed Arthropoda). *Liwia* had four thoracic segments, and the relatively narrow axis is strongly defined on the dorsal surface of the pygidium of *L. convexa*. *Liwia convexa* may well be anonymous with *L. plana* from the same horizon (*fide* Dzik and Lendzion 1988, p. 35), which is known from articulated material. Whether or not this is the case, *Liwia* has free spines on the pygidial margin, and the segmental boundaries are not defined on the pleural fields of the pygidium, as they are in *Soomaspis*. The spines on the pygidium of *Liwia* are probably homologous with the segmental boundaries on *Soomaspis*. There are five pairs on the former which may indicate a similar segmental number to *Soomaspis*, if they were developed on each segment. Whittington (1977) described seven pairs of marginal spines on *Naraoia spinifera* Walcott from the Burgess Shale. Considering that they are stratigraphically so far apart, *Soomaspis* and *Liwia* are remarkably similar. The differences in the thorax and pygidium are considered enough to separate them at generic level, although this judgement could be modified when more is known of *Liwia*.

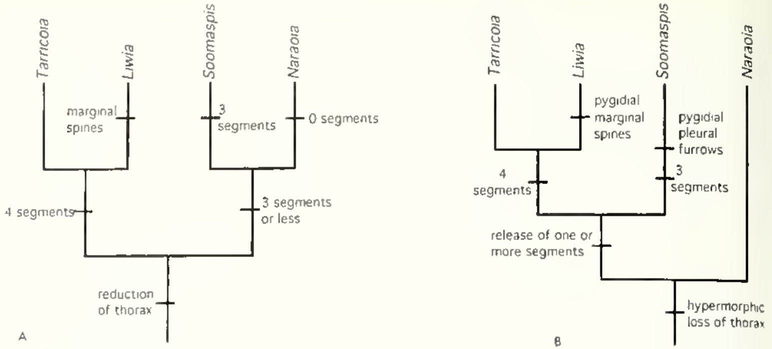
RELATIONSHIPS WITHIN NARAOIIDAE

It is possible to make suggestions as to the relationships between the naraoiid genera (Text-fig. 2). Because there are so few characters, however, these relationships are open to more than one interpretation, and the morphology-based tree differs from that based on stratigraphy. For this level of analysis, no particular purpose is served in using computer based phylogenetic programmes such as PAUP. It is generally thought that the presence of free thoracic segments is the more primitive condition in arthropods (e.g. Hessler and Newman 1975; Briggs and Fortey 1989). If this is the case, then *Naraoia*, in which there are no free segments, is more derived than other naraoiids considered here. This interpretation would suppose that, as in all trilobites, release of thoracic segments occurred from the forward edge of the pygidium (Whittington 1959). This process is suppressed in *Naraoia*. Such an evolutionary scenario makes sense, because the dimensions of pygidium-plus-thorax in relation to the cephalic shield in *Soomaspis* comes close to that of pygidium to cephalon in such *Naraoia* species as *N. spinosa* (Zhang and Hou 1985, pl. 4, fig. 1); in other words, the *Naraoia* pygidium might 'contain' the thorax (Briggs and Fortey 1992, p. 366), which is expressed in *Soomaspis* other liwiines. If this thoracic reduction is accepted as an important advanced character then the cladogram shown on Text-fig. 2A summarizes the relationships between genera.

It should be noted that the branching order in this tree bears no relationship to the stratigraphical order of appearance of the genera; if anything, rather the reverse, because the four-segmented *Tarricoia* is stratigraphically young.

To bring the inferred relationships more in line with stratigraphical order, we have to make an opposite assumption about the genesis of the thoracic segments. This assumption is that the no-segment condition of *Naraoia* was attained at a single mutation by a process of hypermorphosis (see below) of the larval state – equivalent to becoming a huge degree 0 meraspis. Then the release of free segments becomes instead a derived condition – a reversal of what would otherwise be considered the normal character polarity. This results in the hypothesis of relationships shown in the cladogram (Text-fig. 2B). This version has the appeal that the youngest genus (*Soomaspis*) is also that with the best expressed post-cephalic segmentation, notably the only one in which the pygidial pleural fields show clear intersegmental boundaries.

In the context of general arthropod phylogeny, the cladogram on Text-figure 2A is the more acceptable, particularly if parsimony is the arbiter as is usual in cladistic methods. The character

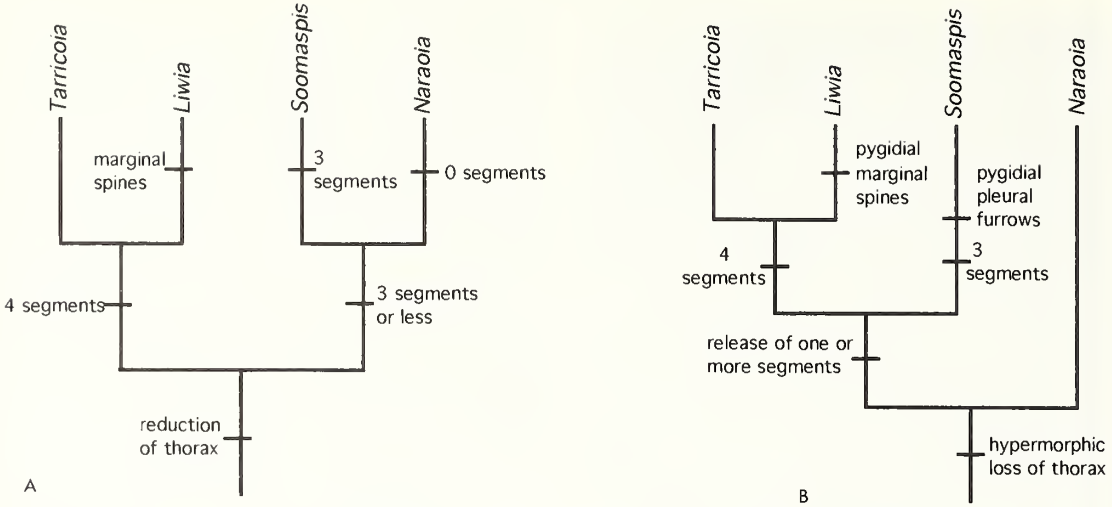


TEXT-FIG. 2. Two hypotheses of relationships between genera within Naraoiidae as understood here. A, assumes more thoracic segments are primitive. B, assumes that the condition in *Naraoia* was primitive, and release of thoracic segments progressive.

polarity 'reversals' involved with the alternative (Text-fig. 2B) are difficult to prove. The occurrence of *Liwia*, with four free segments, early in the Cambrian, rather reduces the force of the stratigraphical argument, although it remains true that *Naraoia* is far more widely known in Cambrian strata. With rather few characters, and rare occurrences of fossils, one should perhaps be cautious about reading too much into stratigraphical sequence. However, it will be interesting to see whether further naraoiids are discovered at other stratigraphical levels, for example in the later Cambrian or early Ordovician, which are more consistent with placing *Naraoia* as the sister group of advanced naraoiids rather than a genus with free thoracic segments. As to function, D. E. G. Briggs has observed (written communication, 1994) that a fused carapace would have served as a support for the massive gnathobases which *Naraoia* is known to have possessed.

HETEROCHRONIC PROCESSES IN THE ORIGIN OF NARAOIIDS AND AGNOSTIDS

The importance of heterochronic processes in generating new morphologies in Cambrian trilobites has been demonstrated by McNamara (1978, 1981). Both naraoiids and agnostids have few thoracic segments and large pygidia, which suggests that paedomorphic processes, in the broad sense, may plausibly account for their peculiar characteristics. This idea has been in currency for a very long time. For example, Salter (1873, p. 48) remarked of '*Agnostus trinodus*' that 'it represents well the embryonic forms of larger trilobites'. What Salter implied was that the release of segments during normal trilobite ontogeny was somehow 'arrested' at an early stage in agnostoids. A more refined classification of heterochronic processes (Gould 1977; summarized in McKinney and McNamara 1991) has permitted critical scrutiny of the timing of developmental shifts. Such changes may be important in rapid appearance of new *baupläne*, not least because a single change at a gene which operates developmental timing may effect profound changes in morphology without the evolution of new, complex organs. Such changes operate upon what is already implicit in the genome. In the discussion which follows, we have used the size of descendent adult as a proxy for time, because we do not have independent evidence for maturation times in trilobites. This seems reasonable given the striking size differences in the trilobites under comparison.



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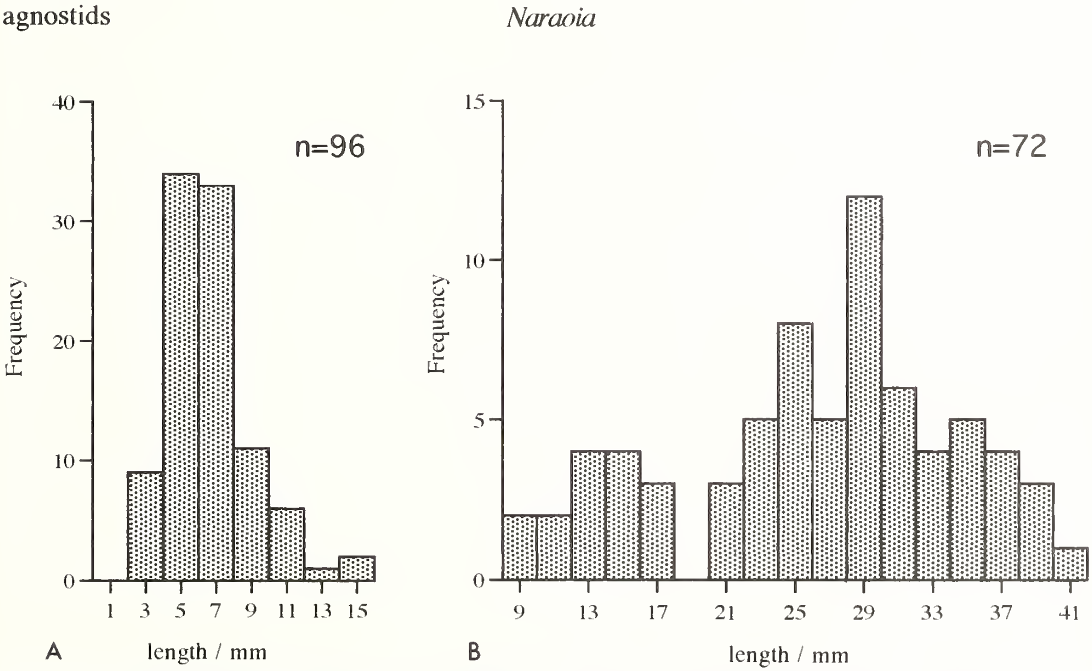
The importance of heterochronic processes in generating new morphologies in Cambrian trilobites has been demonstrated by McNamara (1978, 1981). Both naraoiids and agnostids have few thoracic segments and large pygidia, which suggests that paedomorphic processes, in the broad sense, may plausibly account for their peculiar characteristics. This idea has been in currency for a very long time. For example, Salter (1873, p. 48) remarked of '*Agnostus trinodus*' that 'it represents well the embryonic forms of larger trilobites'. What Salter implied was that the release of segments during normal trilobite ontogeny was somehow 'arrested' at an early stage in agnostoids. A more refined classification of heterochronic processes (Gould 1977; summarized in McKinney and McNamara 1991) has permitted critical scrutiny of the timing of developmental shifts. Such changes may be important in rapid appearance of new *baupläne*, not least because a single change at a gene which operates developmental timing may effect profound changes in morphology without the evolution of new, complex organs. Such changes operate upon what is already implicit in the genome. In the discussion which follows, we have used the size of descendent adult as a proxy for time, because we do not have independent evidence for maturation times in trilobites. This seems reasonable given the striking size differences in the trilobites under comparison.

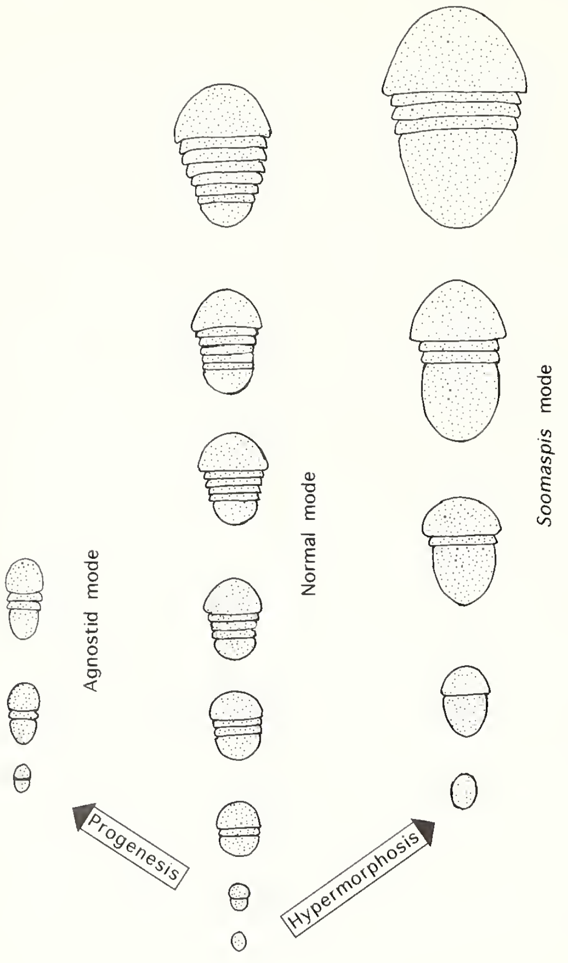
Agnostids

Agnostids are invariably small. A figure for the average length of the agnostid dorsal exoskeleton has been calculated using the most comprehensive recent monograph featuring well-preserved examples from the mid-Cambrian acme of the group (Öpik 1979). This work figures some ninety-six articulated specimens, distributed amongst almost as many species, which are well enough preserved to give a measure of dorsal exoskeletal length. Specimens referred to by Öpik as 'immature' are excluded. If anything, this will bias on the large side, because authors naturally tend to choose larger specimens for illustration. The average length is 6·7 mm, and 90 per cent of specimens fall between 5 mm and 10 mm. The largest figured specimen in Öpik's work is 17 mm. One *can* find larger agnostids, especially among the smooth taxa. The largest known agnostid may be '*Phalacroma*' *glandiforme* (Angelin); an entire specimen illustrated by Westergaard (1946, p. 15, fig. 13) is 20 mm long, and a cephalon (Westergaard 1946, p. 15, fig. 6) indicates that this species may have grown even larger. However, these are most exceptional among Agnostina, on the 'tail' of the upside of a normal distribution curve (Text-fig. 3), and most species are 10 mm or less. Nor is there any obvious trend towards size increase with time, because the youngest Ordovician agnostid, *Arthrorhachis tarda* (Barrande), does not attain any greater length than its Cambrian relatives.



TEXT-FIG. 3. Size frequency histograms. A, trilobites of the suborder Agnostina, based on complete trilobites of broadly comparable age illustrated by Öpik (1979), B, *Naraoia*, based on Whittington (1977).

This indicates that the agnostids are, in terms of heterochronic development, *progenetic* (Briggs and Fortey 1992, p. 348). They are like several other well-known trilobites, *Shumardia* and *Schmalenseeia* perhaps being the classic examples (McNamara 1983; Fortey and Rushton 1980), in which reproductive maturity has been achieved relatively earlier than in the ancestor, usually at a smaller size. This is a precocious onset of the maturation process relative to the ontogenetic



TEXT-FIG. 4. Different heterochronic origins of agnostids and naraoiids (exemplified by *Soomaspis*), the former progenetic, the latter hypermorphic, as compared with a simplified ontogenetic trajectory of 'normal' trilobite type.

trajectory. Agnostids were probably able to reproduce at smaller size than most trilobites, which may have had advantages for organisms which have been claimed as part of the Early Palaeozoic plankton (Robison 1972).

Once this heterochronic change was attained it apparently could not be reversed. The developmental pathway was 'committed' (Reidl 1978). Hence the small size of agnostids is not only because natural selection acted to keep them small; it is also a product of the phylogenetic history of the group, which is progenetic.

Naraoiids

Naraoiids differ from the agnostids in that their size is no different from that of a 'normal' trilobite. Whittington's (1977, text-fig. 2) measurements provide quantitative data on the length of *Naraoia* which can be compared with the agnostoid data herein (see Text-fig. 3). He showed a normal curve with a peak at 30 mm, and a maximum size a little over 40 mm. Zhang and Hou's (1985, pl. 1, fig. 1) Lower Cambrian naraoiid from China is also 40 mm long. Allowing for distortion, specimens of *Tarricoia* are commonly about 30 mm long; *Soomaspis* are mostly about 20 mm long. In short, the size of mature naraoiids begins at the dimensions at which agnostids end, and at four or five times their average size.

This size difference is more than trivial, because it is likely to result from the operation of a different heterochronic mechanism. What has happened in the naraoiids is that the larval growth trajectory has *increased* in size, so that the adult morphology shares larval characteristics by virtue of their being displaced into large individuals. This is the process described as *hypermorphosis*. Although this results in mature individuals with 'larval' characteristics, as in the agnostoids, the kinetics of the process is entirely different from the one pertaining in that group (Text-fig. 4). As we have seen, the one cannot and does not change into the other, because the developmental pathways are fixed once the ancestral condition has been lost. The kinetics of hypermorphosis and progenesis are opposite, but this has not prevented confusion between the different, broadly paedomorphic mechanisms, as McKinney and McNamara (1991) have described.

The interpretation of naraoiid phylogeny makes some difference to the way one interprets this hypermorphosis. If *Naraoia* itself is taken as the first naraoiid (as in Text-fig. 2B), then the degree of hypermorphosis is prodigious: essentially, *Naraoia* is a massively inflated 'degree 0' meraspis. It is interesting to note in this connection Hou *et al.*'s (1991) description of an enormous protaspis (see Text-fig. 1D) from the Lower Cambrian of China, which they attributed to *Naraoia*. This is what would be expected under a hypermorphic hypothesis. The hypermorphosis necessary if *Soomaspis* or *Tarricoia* are considered to be the primitive member of the clade is less, but still considerable, because degree 3 or degree 4 meraspides of other trilobites are only a few millimetres long, at most (Whittington 1959).

Homologies between agnostids and naraoiids

The further implication of such different origins for naraoiids and agnostids is to call into question assumptions about the status of characters which could be claimed as homologies between these two groups. At first glance, the general resemblance between agnostoids and naraoiids is compelling, especially if *Tarricoia* and *Soomaspis* are incorporated into the family as we advocate. However, if their heterochronic origin is different, it is possible that shared resemblances are, after all, homoplasies.

The case of blindness will serve as an example. Both Agnostina (Agnostidae, etc.) and Naraoiidae are blind. Blindness in arthropods is secondary, not primitive, and therefore loss of eyes is a potential synapomorphy of a clade. However, if Eodiscina are related to Agnostina, this group includes species *with* well developed dorsal eyes. But this group is also progenetic (small size, few segments, etc.), and plesiomorphic in other characters, which provides both a developmental link with the Agnostina and evidence that eye loss in the progenetic line (Agnostina) is possibly separate from that in the hypermorphic line (naraoiids).

THE AGNOSTID PROBLEM

Trilobites of the suborder Agnostina are common and varied fossils in Cambrian and Ordovician rocks. Their relationship to more conventional trilobites has always been controversial, and continues to be so. The problem centres upon whether they are trilobites at all, or constitute a distantly related group with a 'separate' ancestry. Allied to this is the question whether typical agnostids (Agnostina, with some ten families according to Shergold *et al.* 1990) are or are not related to Eodiscina, a group which is not disputed as belonging to the Trilobita. Naraoiids come into the argument because they resemble agnostids sufficiently to be regarded as the possible sister group of agnostids and other trilobites (Ramsköld and Edgecombe 1991).

It is not in question that Agnostina were highly specialized arthropods, with a whole series of autapomorphies. This has become particularly clear since the description of the appendages of *Agnostus pisiformis* by Müller and Walossek (1987). For example, the limbs of this agnostid are more individually specialized than in known typical trilobites, and the exites in particular are somewhat reduced. Of exoskeletal structures, the agnostid thorax is peculiar and unique, both with regard to articulation and in losing the first thoracic half-ring, which produces a cephalothoracic aperture during enrollment. No example of an agnostid protaspis has been discovered, although 'degree 0' meraspides are well-known, which implies an idiosyncrasy in its development. However, impressive though these differences are, they do not solve the problem of agnostid relationships, which have to be based on an evaluation of characters which agnostids *share* with other arthropods. After all, it is possible that these peculiarities were largely adaptations for their undoubted specializations, whether these were for planktonic life (Robison 1972), or as ectoparasites (Bergström 1973), or as ostracode-like epibenthos (Pek 1972). In the same way, living copepods and ostracodes are diminutive arthropods with many individual peculiarities, but their relationships within the phylum are determined by the crustacean homologies they share with more conventional relatives.

The three main hypotheses concerning the agnostid problem may be summarized as follows.

1. Agnostids are *not* trilobites. Their resemblance to eodiscines is a matter of convergence (Shergold 1991; Ramsköld and Edgecombe 1991, text-fig. 1). True trilobites include the eodiscines, which were derived from some ptychoparioid ancestor. This view of agnostids has had a long tradition among North American palaeontologists, for example, as stated by Resser (1938, p. 47), 'This group of Crustacea...a subclass parallel to the Trilobita'. Recently, some workers of this persuasion have favoured a more open verdict on the origin of agnostids, preferring to invoke some unknown (presumably Precambrian) ancestor (Shergold 1991; Walossek and Müller 1990). Ramsköld and Edgecombe (1991) portrayed the agnostids as a sister group of restricted Trilobita.

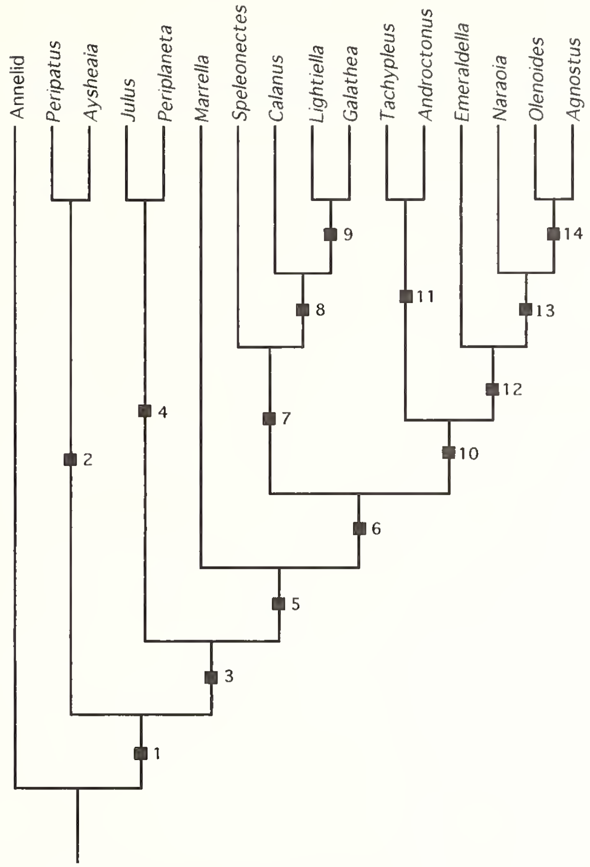
2. Agnostids *are* trilobites, and Eodiscina are their sister group. This clade is more closely related to other trilobites than to naraoiids. This view is implicitly that adopted in the *Treatise on Invertebrate Paleontology*, and was explicitly examined by Fortey (1990). Fortey analysed the problem cladistically, and found more characters supporting a clade Agnostina-plus-Eodiscina, than assuming separate origins for these groups. He placed this clade within Trilobita above olenelloids. Fortey and Whittington (1989) and Ramsköld and Edgecombe (1991) concurred that olenelloids were trilobites, *contra* Lauterbach (1983).

3. Agnostids *are* trilobites, and were derived from more than one eodiscoid group. This view was expressed most recently by Zhang *et al.* (1980, text-fig. 7); it would render the Agnostina polyphyletic. This view does not require further discussion here because, if it were true, nobody disputes that eodiscids (and hence agnostids) are trilobites. However, it does seem that the long list of agnostid autapomorphies (e.g. Fortey 1990; Müller and Walossek 1987) makes it probable that they are a monophyletic group.

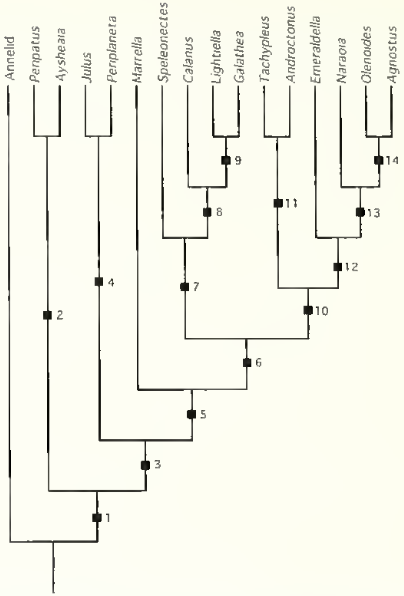
Character analysis is the correct way to resolve these competing hypotheses, but this is not as simple as it may seem, because not all the relevant fossils have full information available; for example, limbs are not known for all the groups, e.g. eodiscoids. Character analysis of the taxa for which only hard parts are available does not necessarily yield the same result as those for which complete skeletal information is known.

Whole organism approach to the agnostid problem

Using examples of taxa for which limbs have been described generates a large character matrix for which parsimony methods of cladistic analysis (such as PAUP) are appropriate. Several attempts to place agnostids within the arthropods as a whole have been attempted, using progressively refined character definitions (Briggs and Fortey 1989; Briggs, Fortey and Wills 1992; Wills, Briggs and Fortey 1994). These cladistic analyses included agnostids as one of more than forty arthropods, including both Burgess Shale species and primitive members of extant groups, for which the coding of many homologous skeletal and appendage characters was practicable. All the most parsimonious trees from all the analyses included agnostids together with naraoiids and higher trilobites (represented by *Olenoides*) in the same clade. This clade could be termed Trilobita. In this sense, trilobites occupied a rather advanced position on all trees, comprising a sister group to limuloids and other Arachnida, while crustaceans and crustacean-like arthropods resolved at lower nodes. A simplified version of this analysis is shown in Text-figure 5, a unique solution with the taxa chosen,



TEXT-FIG. 5. Cladogram of trilobites and selected arthropods belonging to other major groups, based on coding of characters of whole organism (full data given in Wills *et al.* 1994), including limbs. *Naraoia* is the sister group of other trilobites, including *Agnostus*. Synapomorphies listed below are not coded individually, but are summarized for each branch. 1, Inner rami of trunk appendages present. 2, Inner rami of appendages of second post-acronal somite present; inner rami of trunk appendages with a terminal group of claw-like reflexed spines; terminal trunk division with appendages. 3, Cuticle sclerotized; labrum present; increase from one to five post-acronal somites incorporated into the cephalon; trunk appendages sclerotized and stenopodous. 4, Compound eyes present; appendages of third post-acronal somite modified as mandibles biting with their tips; tracheae present. 5, Cephalic shield entire or as a single unit followed by a variable number of associated tergites; presence of a doublure; inner rami of appendages of second post-acronal somite present; outer rami of trunk appendages present. 6, Appendages of third post-acronal somite with gnathobases. 7, Outer rami of appendages of second post-acronal somite present; appendages of third post-acronal somite modified as gnathobasic mandibles; terminal trunk division with appendages. 8, Appendages of second post-acronal somite antenniform; filaments absent from the outer rami of trunk appendages. 9, Post-cephalic articulation with overlapping pleurae; differentiation of an abdomen; trunk appendages with distinctive epipodites; gut diverticulae present. 10, Increase from five to six post-acronal somites incorporated into the cephalon; outer rami of trunk appendages unsegmented. 11, Median eye present; appendages of first post-acronal somite modified as chelicerae; appendages of second post-acronal somite modified as pedipalps; anus ventral in the penultimate division of the body; terminal body division styliform. 12, Post-cephalic articulation with overlapping pleurae; inner rami of trunk appendages spinose; trunk appendages with gnathobases or protopodal endites; outer rami of trunk appendages with distal lobe. 13, Trilobation; marginal rim present; pygidium present; reduction from six to four post-acronal somites incorporated into the cephalon; outer rami of appendages of second post-acronal somite present; anus ventral in the terminal division of the body; gut diverticulae present. 14, Cuticle mineralized with calcium carbonate; genal spines present; differentiation of an abdomen.



TEXT-FIG. 5. Cladogram of trilobites and selected arthropods belonging to other major groups, based on coding of characters of whole organism (full data given in Wills *et al.* 1994), including limbs. *Naraoia* is the sister group of other trilobites, including *Agnostus*. Synapomorphies listed below are not coded individually, but are summarized for each branch. 1, Inner rami of trunk appendages present. 2, Inner rami of appendages of second post-acronal somite present; inner rami of trunk appendages with a terminal group of claw-like reflexed spines; terminal trunk division with appendages. 3, Cuticle sclerotized; labrum present; increase from one to five post-acronal somites incorporated into the cephalon; trunk appendages sclerotized and stenopodous. 4, Compound eyes present; appendages of third post-acronal somite modified as mandibles biting with their tips; tracheae present 5, Cephalic shield entire or as a single unit followed by a variable number of associated tergites; presence of a doublure; inner rami of appendages of second post-acronal somite present; outer rami of trunk appendages present 6, Appendages of third post-acronal somite with gnathobases. 7, Outer rami of appendages of second post-acronal somite present; appendages of third post-acronal somite modified as gnathobasic mandibles; terminal trunk division with appendages. 8, Appendages of second post-acronal somite antenniform, filaments absent from the outer rami of trunk appendages. 9, Post-cephalic articulation with overlapping pleurae; differentiation of an abdomen; trunk appendages with distinctive epipodites; gut diverticulae present. 10, Increase from five to six post-acronal somites incorporated into the cephalon; outer rami of trunk appendages unsegmented. 11, Median eye present; appendages of first post-acronal somite modified as chelicerae; appendages of second post-acronal somite modified as pedipalps; anus ventral in the penultimate division of the body; terminal body division styliform 12, Post-cephalic articulation with overlapping pleurae; inner rami of trunk appendages spinose; trunk appendages with gnathobases or protopodal endites; outer rami of trunk appendages with distal lobe. 13, Trilobation; marginal rim present; pygidium present; reduction from six to four post-acronal somites incorporated into the cephalon; outer rami of appendages of second post-acronal somite present; anus ventral in the terminal division of the body; gut diverticulae present. 14, Cuticle mineralized with calcium carbonate, genal spines present; differentiation of an abdomen.

TABLE 1. List of characters of exoskeleton used to produce cladistic analyses on Text-figures 7 and 8. Note that the coding on character 17 is changed as shown in square brackets to produce the coding for Text-figure 8.

1 Glabella: defined dorsally (1), not defined dorsally (0).
2 Few thoracic segments – by progenesis (1), by hypermorphosis (2). Normal number of thoracic segments (0).
3 Thoracic articulation: trilobite style (1), agnostoid style (2), poorly developed articulation (0).
4 Doublure on cephalon: wide (0), narrow, reduced (1).
5 Hypostome: present (1), absent (0).
6 Hypostome condition: natant (1), conterminant (0). Note: the homology of hypostome and the labrum in *Tachypleus* is dubious and the coding given for the latter in Table 2 is a default coding.
7 Cuticular terrace ridges on venter: present (1), absent (0).
8 Calcified protaspis: present (1), absent or unknown (0).
9 Pygidium: present (1), absent (0).
10 Dorsal eyes: present (0), absent (1).
11 Calcified cuticle: absent (0), present (1).
12 Eyes comprising calcite prisms: absent (0), present (1).
13 Cephalon matching pygidium closely in proportions and outline: yes (1), no (0).
14 Dorsal facial sutures: absent (0), opisthoparian (1), proparian (2).
15 Palpebro-ocular ridges: absent (0), present (1).
16 Genal spines: present (0), absent (1). Note: genal spines are secondarily developed on some Agnostina (e.g. *Triplagnostus*); these may or may not be homologous with those on other trilobites, but are present on neither of the taxa coded here.
17 Rostral plate: absent (0), present (1), [secondarily lost (2)].
18 Occipital width: exceeds width of glabella in front (1), does not exceed (0). Note: the agnostoid occipital ring is understood to include the triangular lateral lobes.
19 Cephalic shield long, sagittal length equal to, or exceeding transverse width (which is often anterior to posterior cephalic margin) (1), cephalic shield wider than long, and with maximum width at posterior margin (0). (Note: the progenetic *Olenelloides* provides one exception.)
20 Cephalic border: 'rolled' (1), flattened (2), border absent (0).
21 Connective sutures: present (1), absent (0).
22 Pygidial length: exceeding cephalic (1), less than or subequal (0).

with a tree length of 149. This cladogram uses the characters and coding discussed at length in Wills *et al.* (1994), to which the reader is referred for details. In the present context there is no particular purpose in including *all* the other Burgess type arthropods, and this cladogram includes only two arachnids, including a limuloid (*Tachypleus*), five arthropods with crustacean-like bodyplans (the clade *Galathea* to *Speleonectes*); the lobopods, *Aysheaia* and *Peripatus*, and an annelid are outgroups. With a consistency index (excluding uninformative characters) of 0·51 this tree is better supported than the more inclusive trees published previously (Briggs *et al.* 1992). The trilobite clade is quite well defined. The Burgess Shale arthropod *Emeraldella* occupies the position as sister taxon to the Trilobita. Synamorphies are listed in the legend to Text-figure 5.

This treatment gives *Naraoia* as the sister group of higher trilobites, a clade comprising *Agnostus* and *Olenoides*. It would be possible, if one wished, to exclude *Naraoia* from the trilobites by appropriate definition (a view like that of Ramsköld and Edgecombe 1991) although this would not be our recommendation. The naraoiids are consistently associated with other arthropods regarded as trilobites in all other analyses (e.g. Briggs *et al.* 1992) and it seems to us unwise to proliferate taxa at the highest level. Furthermore the Trilobita, including naraoiids, comprise a clade equivalent to other clades conventionally regarded as classes or subphyla (Arachnida, for example).

The question of how agnostids relate to Eodiscina cannot be resolved by this kind of analysis, because the latter are not known from specimens showing ventral limb morphology. Are agnostid peculiarities a product of progenesis? A similar case among Crustacea is the difficulty of recognizing the sister group of Copepoda (Schram 1986). To examine this problem in an appropriate way we next analyse the agnostids in relation to other Cambrian trilobites, including naraoiids, olenellids, redlichiids and eodiscoids, which have been cited as relevant to the 'agnostid problem'.

Walossek and Müller (1990) noted resemblances between *Agnostus* and what they termed 'stem group Crustacea' from the Upper Cambrian *Orsten* of Sweden. The most impressive of these are apparent limb homologies between *Henningsmoenia* and *Agnostus*; the former also had a hypostome. However, *Henningsmoenia* is a minute arthropod, with an enlarged dorsal shield, and its position within the 'stem arthropod' complex is at least as difficult to decide as that of agnostids. It does not have a pygidium, neither are its eyes included in the dorsal shield, nor is its carapace calcified. Five pairs of cephalic limbs are more than is characteristic of trilobites, or *Agnostus*. It is interesting to note the resemblance between the shield of *Henningsmoenia* and the minute, phosphatized carapace regarded as a 'pre-protaspis' (phaselus) trilobite larva by Fortey and Morris (1978). It is possible that the minute *Henningsmoenia*, too, is progenetic, and that the limb resemblances between it and agnostids betray a similar ontogenetic ancestry.

Exoskeletal characters and the agnostid problem

In order to examine the relationships of agnostids using a wider variety of relevant trilobites, it is a requirement that characters of the exoskeleton are used, because several of the trilobites concerned are not known with appendages preserved. Fortey (1990) considered this problem, using his own judgement on relevant synapomorphies, and without the inclusion of naraoiids in the analysis. Here we analyse the problem using a computer based parsimony analysis (PAUP *vs.* 3·1). Olenellids are accepted as trilobites (Fortey and Whittington 1989; Ramsköld and Edgecombe 1991). A limuloid is the outgroup. The new naraoiid, *Soomaspis*, is included, not least to establish that our view of its inclusion within the same clade as *Naraoia* is justified. Characters used are shown in Table 1 and their coding in Table 2.

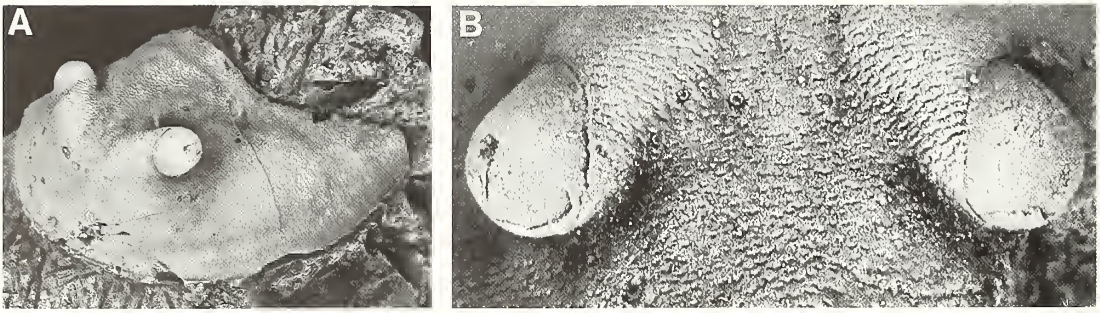
TABLE 2. Coding of characters given in Table 1 for the cladogram, Text-figure 7. See text for further discussion.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Naraoia	0	2	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	?	0	0	0	1
Soomaspis	0	2	0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	?	0	0	1	1
Agnostus	1	1	2	1	1	1	0	0	1	1	1	0	1	0	0	1	0	1	1	1	0	0
Pagetia	1	1	1	1	1	1	0	1	1	0	1	1	1	2	1	1	0	1	1	1	0	0
Tril (*Olenoides*)	1	0	1	0	1	0	1	1	1	0	1	1	0	1	1	0	1	0	0	2	1	0
Olenellus	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	0	2	0	0
Tachypleus	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	?	0	0	0	0

It should be noted that there are some differences in character interpretation between Fortey and Whittington (1989) and Ramsköld and Edgecombe (1991). The former were concerned primarily with the place of olenelloids (then being studied by Whittington, see Whittington 1989) within the Trilobita, as opposed to claims (e.g. Lauterbach 1983) that some olenellids were more closely related to limuloids and other arachnoids than to Trilobita *sensu stricto*. *Naraoia* was specifically omitted from the discussion, an omission that Ramsköld and Edgecombe (1991) regarded as 'unfortunate'. In fact, one of us was already addressing the problem of the place of naraoiids (and agnostids) in a different publication (Briggs and Fortey 1989) as the first of several analyses using a wider spectrum of arthropods. These studies dealt with problems concerning outgroup definitions raised by Ramsköld and Edgecombe (see Smith 1994). However, some of the characters used by Fortey and Whittington are used again herein, and the comments of Ramsköld and Edgecombe need brief reference, especially where there are factual errors. The following comments also encompass points made by Shergold (1991).

1. Pygidium. The possession of a pygidium comprising two or more fused segments was regarded by Fortey and Whittington (1989) as a typical trilobite character. Ramsköld and Edgecombe (1991) stated that the 'pygidium' of *Olenellus* had only one segment (regarded as a possible autapomorphy of Olenellidae). However, Whittington (1989, p. 119) described the pygidium of the type species of *Olenellus*, *O. thomsoni* – the reference point for discussions of olenellid anatomy – as including more than one segment, because 'inter-ring furrows' were recognized, and mentioned in his description. It is widely recognized that there *are* examples in undoubted Trilobita where the release of thoracic segments into the thorax proceeds to the point where only a single posterior plate remains (e.g. *Celmus*, see Bruton 1983), but this is secondary. But this is not true of *O. thomsoni*, even if it may apply to other olenellids.

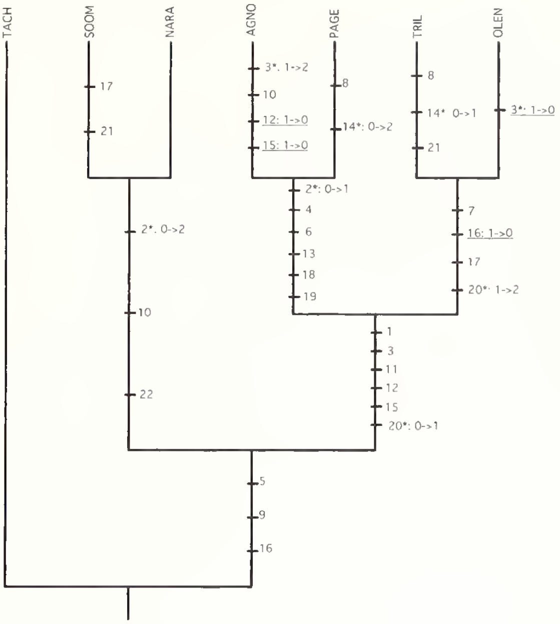
2. Calcified lens structure. The trilobite eye is uniquely constructed. Fortey and Whittington scored the eye as a character separate from calcification of the cuticle, a view which was criticized by Ramsköld and Edgecombe (1991) on the grounds that it was 'unknown whether [eye structure] can be treated as an independent apomorphic character'. They state that 'the mineralogy and optical axis are two characters that are obligately coupled in trilobites'. However, the prismatic structure of the calcified corneal surface differs fundamentally from laminated structure elsewhere in the cuticle (Clarkson 1975). Furthermore, because primitive trilobites have a circum-ocular suture, there was really no obligation for the corneal surface to behave in the same way as the rest of the cuticle. An example of an undescribed aglaspid with calcified cuticle but apparently phosphatic corneal surface (Text-fig. 6) illustrates this decoupling. It seems rather unlikely to us that calcification of the cuticle *and* the specialized structure of the corneal surface could have been achieved as a single mutation. Nor do other calcified arthropods (ostracodes, decapods) solve their optical problems in the same fashion as trilobites. Fortey and Whittington (1989) were probably entitled to regard optical and cuticular characters separately.



TEXT-FIG. 6. Eye of an undescribed Chinese Silurian aglaspid showing difference in composition from calcareous cuticle. The eye is phosphatic, but this may be after a different original matrix. A, anterior oblique view of prosoma; × 4; B, detail of eyes, dorsal view; × 8. (Photographs supplied by Dr Derek J. Siveter).

3. Rostral plate. Detailed comments on the importance of the rostral plate were given by Fortey (1990). Evidence for a rostral plate in *Soomaspis* is discussed above, but for other naraoiids the evidence is equivocal. The *Naraoia* species illustrated by Zhang and Hou (1985, pl. 1) clearly shows the hypostome in conterminant attachment mode, but it is hard to assess whether the rostral plate is a separate structure, or whether the doublure is in continuity with the dorsal surface. Note that Ramsköld and Edgecombe (1991, fig. 1), show 'rostral plate' as a synapomorphy of Eodiscoidea and 'more derived trilobites', whereas the former group apparently lacks such a plate (Jell 1975, pl. 1, fig. 1; see also Fortey 1990, text-fig. 13).

4. Hypostome. Fortey and Whittington (1989) cited the hypostome, together with anterior wings that articulate against the fossulae in the axial furrows, as a trilobite character. It is a complex structure, which might have been 'broken up' into more than one character, but does indeed seem



TEXT-FIG. 7. Cladistic analysis of relationships of agnostids to naraoiids and other trilobites based on the character matrix given in Table 2. Characters listed in Table 1. This version does not assume that agnostids and eodiscids had an *Olenellus*-like rostral plate which was secondarily lost. Tree length = 34 steps; Consistency Index = 0·77. PAUP *vs.* 3·1, on Mackintosh. On this and the following figure character reversals are indicated by asterisks, and changes in multi-state characters are underlined.

to be characteristic of an enormous range of trilobites (Whittington 1988*a*, 1988*b*; Fortey 1990). Ramsköld and Edgecombe (1991) cast doubt on whether the trilobite and agnostid hypostome were truly homologous, basing their arguments mostly on *Agnostus* (Müller and Walossek 1987). They may have been unaware that Robison (1988, fig. 9) described a hypostome of *Oidalagnostus trispinifer*, complete with wings, which is similar to that of *Pagetia* (Eodiscina) (see Jell 1975), and also like that of many ptychopariids. The hypostome of *Naraoia* has been figured by Zhang and Hou (1985, pl. 1). It would certainly be good to know more about hypostome-like structures of likely trilobite sister taxa, as Ramsköld and Edgecombe say, and this will serve to focus future work. However, it does seem to go against common sense to assume that a complex structure like the hypostome evolved entirely in parallel between pagetiids and other trilobites on the one hand, and agnostids on the other.

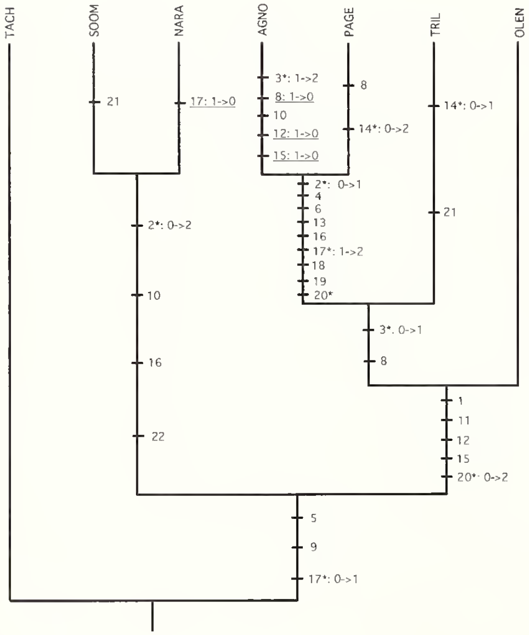
5. Larval characteristics. Much has been made by Shergold (1991) of the fact that pagetiids (Eodiscoidea) had calcified protaspid larvae (see also Zhang 1989). Neither agnostids nor olenellids had calcified protaspides, so far as is known. This character, in particular, is cited as evidence that eodiscoids and agnostids had separate phylogenetic origins, the former within a clade of 'higher' trilobites, the latter with a separate trilobite-like ancestor within that grade of organization at which protaspides had not yet calcified. The results of our analysis indicate an alternative hypothesis, which includes pagetiids and agnostids as sister groups, which then supposes the non-calcification of the agnostid protaspis to be secondary, perhaps another consequence of progenesis.

The three different hypotheses for agnostid relationships have different consequences for future discoveries. Shergold's (1991) view predicts that no calcified agnostid protaspis shall ever be discovered, nor any eodiscoid discovered without one. Zhang *et al.*'s (1980) polyphyletic view predicts that calcification was lost more than once, hence, presumably, early agnostids might still retain a calcified protaspis, and/or the appropriate eodiscoid ancestor may already have lost it. The hypothesis supported here shows that no eodiscoid should be without a calcified protaspis, but it remains possible that not all the autapomorphies supporting the agnostid clade were acquired at the same time, and hence that a primitive agnostid (likely to be stratigraphically lower, in the Lower Cambrian) still retained a calcified earliest growth state. Perhaps the potential resolution of these alternatives will stimulate the hunt for phosphatized or silicified growth stages in the appropriate Lower Cambrian strata.

Agnostid relationships from the new analysis

The analysis of exoskeletal characters resulted in a unique tree with a consistency index of 0·76 (excluding uninformative characters), which indicates good robustness overall. The relationships shown on Text-figure 7 support the inclusion of Agnostina and Eodiscina in a single clade; higher trilobites and olenelloids together constitute the sister taxon of this clade. *Soomaspis* resolves with *Naraoia*, thus supporting the view of Naraoiidae (or Nektaspida) adopted in this paper. Together, they comprise the sister group of the other trilobites, thereby affirming their comparatively primitive position as uncalcified members of the same clade as other trilobites. However, the inclusion of eodiscoids into the analysis reveals the agnostid peculiarities as likely specializations, rather than a consequence of a separate evolutionary history. Those who would defend the latter theory must invoke a less parsimonious explanation for the characters which agnostids and eodiscoids share. Such explanations require much parallel evolution, which has to be demonstrated rather than asserted; the ontogenetic predictions given above may help. Also, if the progenetic explanation of agnostid origins is true, one might anticipate that when limbs of meraspides of eodiscoids and other trilobites are discovered that they may show similarities to those of agnostids.

Fortey (1990) preferred a position for Agnostida above Olenellida. Its position as shown in Text-figure 7 is not particularly strongly supported, and depends very much on the coding of character 17, the rostral plate. In our coding we have followed Müller and Walossek (1987) in assuming that the rostral plate was not present in Agnostida. However, Fortey (1990) preferred to regard this plate as secondarily lost in most Agnostida, probably by decalcification, citing as evidence the rare description of olenellid-like (i.e. with perrostral suture) rostral plates in agnostids (Hunt 1966). Character 7 (terrace ridges on venter) does really depend on cephalic doublure being present, and is not fully independent of character 17. If the data are re-analysed, this time making the assumption that the agnostoid composition was achieved by *loss* of a rostral plate, then the topology shown in Text-figure 8 is obtained, which resembles that of Fortey (1990). This tree is one step shorter than



TEXT-FIG. 8. As for Text-figure 7, but re-analysed on the assumption that agnostids and eodiscids had an *Olenellus*-like rostral plate, which then became lost to induce the natant hypostomal condition. Note how this draws the agnosid clade farther into the higher Trilobita. Tree length = 33 steps; Consistency Index = 0·76.

that in Text-figure 7, and has about the same consistency index, implying that it is, overall, a better solution than that in Text-figure 7. Clearly, it will be crucial to find out more about the ventral morphology of agnostids and eodiscoids to decide between these alternatives. For example, if more cases of olenelloid rostral plates are discovered in eodiscoids or agnostids, the inclusion of Agnostida well within the trilobite clade will receive additional support.

HIGH LEVEL TRILOBITE CLASSIFICATION

There are several ways to classify trilobites at the highest level with regard to the inclusiveness of the group. On the basis of the analysis given here as Text-figure 7, for example, one could regard olenellids and other non-agnostoid trilobites as Trilobita, *sensu stricto*, and exclude both Agnostida, and the Nektaspida. However, this would mean excluding the Eodiscina, which are universally considered to be trilobites. If one followed other cladistic analyses (e.g. Briggs *et al.* 1992) one could possibly include agnostids but exclude naraoiids. Fortey (1990) placed the Agnostida (in which Eodiscina were included) in a higher position in the cladogram than is the case in Text-figure 7 making them undoubted trilobites, as in Text-figure 8. On the contrary, if one followed Shergold (1991), one could include Eodiscina in Trilobita but exclude Agnostina, since he regarded the resemblances between the two groups as convergence. Walossek and Müller (1990) were altogether uncertain as to where Agnostina fitted into the stem lineage of the arthropods. Although we prefer the analysis given here as the most parsimonious on the basis of exoskeletal characters, it is clearly the case that Agnostina are a controversial group. But they *do* fall in with naraoiids, and other calcified trilobites as a clade in all cladistic analyses, even though their position within the clade may vary. We regard as necessary the inclusion of Eodiscina in any analysis correctly to polarize the characters of agnostids. At the least, for a practical classification, it is unwise to exclude Agnostina from a narrowly-defined Trilobita while their position is still labile according to the approach to classification adopted by one or another researcher.

Inclusion of Naraoiidae within the Trilobita is supported by relatively few characters, as already noted by Ramsköld and Edgecombe (1991). One can make a comparatively long list of characters supporting the rest of the Trilobita (topology as in Text-fig. 7). Nonetheless, the consistent association of naraoiids with the rest of the trilobites in analysis, their ventral and pygidial morphology, and the simplicity of a hypermorphic explanation for their origin, all point to the sense of including them within the Trilobita.

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A MODEL FOR THE MORPHOGENESIS OF RIBS IN AMMONITES INFERRED FROM ASSOCIATED MICROSCULPTURES

by ANTONIO CHECA

ABSTRACT. Eight morphological types of microsculpture have been recognized on the outer shell surface of well-preserved ammonites. They consist mainly of wrinkles and creases which were developed on a pliant material. They are interpreted as the result of compressive stresses which occurred on a free (i.e. uncalcified) periostracum. This is the first evidence of periostracal development in ammonoids, and its relation to the shell suggests a mode of calcification similar to present-day molluscs. This periostracum was also attached to the soft body along longitudinal lines. All microsculptures were compression structures. This, their concentration within intercostal valleys, and additional evidence, leads to the proposal of a new morphogenetic model for ammonite ribs, in which they represent compression folds developed on the free periostracum which were later calcified. Evidence that ribs coincide with growth halts supports this view. An enigmatic feather-like ornament is interpreted merely as a long-wave variant of wrinkling. The study of shell structure implies that the aperture was never fully calcified except at maturity. Therefore, ribs did not reinforce the apertural edge, which was easily torn allowing the ammonite to scape, but rather avoided the peeling of the shell from some distance to the aperture backwards. Differences in timing and mode of calcification existed between constricted and non-constricted ammonites. In fact, the presence of constrictions could indicate episodic growth, similar to that of some Recent gastropods.

AMONG the many varieties of ammonoid ornaments, ribs are the most important elements. They are found from the Palaeozoic onwards, and gained in strength with time (Ward 1981). Despite their structural importance, very few studies have dealt with costal morphogenesis. The only previous morphogenetic study is that by Checa and Westermann (1989) who recognized that, in general, growth lines are perfectly parallel to ribs in Jurassic ammonites, so that the peristome had to change its shape to accommodate the variable costal morphology. These authors called this the segmental growth pattern.

The examination of extremely well-preserved Jurassic and Cretaceous ammonites allowed me to recognize diverse superficial microsculptures, which were originally developed in the external surface of the shell, and arranged and associated in a precise manner. Their interpretation allows us to form a precise picture of the pattern of shell calcification in ammonites and to establish an unexpected model of construction of ribs, which is completely new to shelled invertebrates.

In this paper the term 'microsculpture' is used to describe variously shaped microreliefs developed on the outer shell surface and different from usual ornamentation, such as ribs or tubercles.

MATERIAL

Microsculptures were first observed by the author at the Oxford University Museum in 1989 in an extensive collection of Upper Jurassic *Pavlovia*, from a disused pit in Hartwell, south-west of Aylesbury, Buckinghamshire. Only twelve specimens displayed microsculptures, mainly for preservational reasons. Given the exceptional nature of this material, only one shell sample was studied under SEM, which revealed that the original microstructure had been retained. Microsculptures were also profusely observed in seven Hildoceratinae, one *Peronoceras* and one

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TABLE 1. List of material, with indication of microsculpture(s) recognized (numbers refer to microsculpture description in the text). Specimens labelled C are housed at the Natural History Museum, London; those labelled J or JZ are at the Oxford University Museum. BMNH: Natural History Museum London; DPUG: Departamento de Estratigrafía y Paleontología de la Universidad de Granada; GPIUH: Geologisch-Paläontologisches Institut der Universität Hamburg.

Taxon	Age	Locality	Registration No.	Microsculpture
PHYLLOCERATINA				
Phylloceratacea				
Tragophylloceras ibex (Quenstedt)	Pliensbachian	Watford (Northamptonshire)	C19581, C56638	(2)
T. boblayei (d'Orbigny)	Pliensbachian	Cheltenham (Gloucestershire)	C28215	(2)
T. loscombi (Sowerby)	Pliensbachian	Charmouth (Dorset)	C36714, −848, C55644, C73923, −5	(2)
T. undulatum (Smith)	Pliensbachian	Radstock (Somerset)	C50451	(2)
ANCYLOCERATINA				
Ancylocerataceae				
Crioceratites seelevi (Neumayr and Uhlig)	Hauterivian	Ihme (nr. Hannover)	C14392, −3, −4	(1)
Turrilitaceae				
Baculites chicoensis Reeside	Campanian	Nanaimo (Vancouver Isl.)	C53070	(8)
AMMONITINA				
Psilocerataceae				
Asteroceras confusum Spath	Sinemurian	Bredon (Worcestershire)	C2223	(3)
Caenisites brooki (Sowerby)	Sinemurian	Dorset	C47352	(3)
Oxynoticeras sp.	Sinemurian	—	Unreg. (BMNH)	(2)
Eoderocerataceae				
Androgynoceras maculatum (Young and Bird)	Pliensbachian	Dorset	C63410	(8)
Oistoceras figulinum (Simpson)	Pliensbachian	Kirton (Lincolnshire)	C73534	(1), (5)
Amaltheus stokesi (Sowerby)	Pliensbachian	Stroud (Gloucestershire)	C10380	(8)
Dactylioceratidae sp.	Toarcian	—	Ch.S_1 (DPUG)	(4)
Peronoceras sp.	L. Toarcian	—	C67532	(5)
Peronoceras sp.	L. Toarcian	—	J31943	(1), (4), (5)
Hildocerataceae				
Harpoceras falcifer (Sowerby)	L. Toarcian	Northamptonshire	C68616	(2)
Eleganticeras sp.	L. Toarcian	nr. Hamburg	Unreg. (GPIUH)	(2)
Pseudolioceras sp.	U. Toarcian	—	Unreg. (BMNH)	(2)
Pseudolioceras lithense (Young and Bird)	U. Toarcian	Northamptonshire	C66917, −8, −9	(8)

Osperleioceras sp.	U. Toarcian	—	J30375	(2), (5)
Hildoceras sp.	L. Toarcian	—	J30359	(2)
Hildoceras sp.	L. Toarcian	—	J30356	(8)
Hildoceras sp.	L. Toarcian	—	J30352, −3, −5, −64	(2), (8)
Hildaites sp.	L. Toarcian	—	J30368	(2), (8)
Leioceras sp.	L. Aalenian	Goslar (Harz)	C4880	(2)
Stephanocerataceae				
Kosmoceras castor (Reinecke)	Callovian	—	C7932	(1)
Gulielmites sp.	Callovian	Twyford (Buckinghamshire)	C79439, −40	(8)
Cardioceras sp.	Oxfordian	—	JZ.2224	(8)
Cardioceras sp.	Oxfordian	Staffin (Skye)	C71044	(2)
Amoeboceras rosenkrantzi Spath.	U. Oxfordian	Staffin (Skye)	Unreg. (BMNH)	(2), (8)
Dimorphinites sp.	Bajocian	Yeovil (Somerset)	C52049	(8)
Perisphinctaceae				
Proplanulites sp.	Callovian	—	Unreg. (BMNH)	(8)
Binatisphinctes sp.	Callovian	Kowno (W. Russia)	C7983	(3)
Dichotomosphinctes sp.	Oxfordian	Staffin (Skye)	Unreg. (BMNH)	(3)
Crussoliceras divisum (Quenstedt)	L. Kimmeridgian	Zafarraya (Granada)	Ch.Z1.2b.1 (DPUG)	(5)
Rasenia sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C69820	(1), (3)
Rasenia sp.	L. Kimmeridgian	Horncastle (Lincolnshire)	C69831	(3), (8)
Rasenia sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C69832	(3), (8)
Rasenia sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C70514	(1), (3), (8)
Pararasenia sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C93899	(8)
Pavlovia sp.	Portlandian	Hartwell (Buckinghamshire)	J30355, −68, J35848, −68, −99	(5)
Pavlovia sp.	Portlandian	Hartwell (Buckinghamshire)	J35894, −9	(4), (6)
Pavlovia sp.	Portlandian	Hartwell (Buckinghamshire)	J35857, −87, −91	(1), (5)
Pavlovia sp.	Portlandian	Hartwell (Buckinghamshire)	J35883, −94	(3), (5)
Hoplitaceae				
Hypacanthohoplites jacobi (Collet)	Albian	Vöhrum (Hannover)	C14550	(3), (8)
Placenticeras meeki Boehm	U. Cretaceous	South Dakota	C22686, C40062	(2), (8)
Placenticeras placenta (Dekay)	U. Cretaceous	South Dakota	C31345, C74029	(2), (8)
Placenticeras umkwelanensis Klinger	Coniacian	Zululand	C93898	(2)
Hoplites dentatus (Sowerby)	Albian	Devizes (Wiltshire)	C88627	(7)
Euhoplites sp.	U. Albian	Calais	C92747	(2)

TABLE 1. List of material, with indication of microsculpture(s) recognized (numbers refer to microsculpture description in the text). Specimens labelled C are housed at the Natural History Museum, London; those labelled J or JZ are at the Oxford University Museum. BMNH: Natural History Museum London; DPUG: Departamento de Estratigrafía y Paleontología de la Universidad de Granada; GPIUH: Geologisch-Paläontologisches Institut der Universität Hamburg.

Taxon	Age	Locality	Registration No	Microsculpture
PHYLLOCERATINA				
Phyllocerataceae				
Tragophylloceras ibex (Quenstedt)	Pliensbachian	Watford (Northamptonshire)	C19581, C56638	(2)
T. boblayei (d'Orbigny)	Pliensbachian	Cheltenham (Gloucestershire)	C28215	(2)
T. loscombi (Sowerby)	Pliensbachian	Charmouth (Dorset)	C36714, −848, C55644, C73923, −5	(2)
T. undulatum (Smith)	Pliensbachian	Radstock (Somerset)	C50451	(2)
ANCYLOCERATINA				
Ancylocerataceae				
Crioceratites seeleyi (Neumayr and Uhlig)	Hauterivian	Ihme (nr. Hannover)	C14392, −3, −4	(1)
Turrilitaceae				
Baculites chicoensis Reeside	Campanian	Nanaimo (Vancouver Isl.)	C53070	(8)
AMMONITINA				
Psilocerataceae				
Asteroceras confusum Spath	Sinemurian	Bredon (Worcestershire)	C2223	(3)
Caenisites brooki (Sowerby)	Sinemurian	Dorset	C47352	(3)
Oxynoticeras sp.	Sinemurian	—	Unreg. (BMNH)	(2)
Eoderocerataceae				
Androgynoceras maculatum (Young and Bird)	Pliensbachian	Dorset	C63410	(8)
Oistoceras figulinum (Simpson)	Pliensbachian	Kirton (Lincolnshire)	C73534	(1), (5)
Amaltheus stokesi (Sowerby)	Pliensbachian	Stroud (Gloucestershire)	C10380	(8)
Dactylioceratidae sp.	Toarcian	—	Ch.S$_1$ (DPUG)	(4)
Peronoceras sp.	L. Toarcian	—	C67532	(5)
Peronoceras sp.	L. Toarcian	—	J31943	(1), (4), (5)
Hildocerataceae				
Harpoceras falcifer (Sowerby)	L. Toarcian	Northamptonshire	C68616	(2)
Eleganticeras sp.	L. Toarcian	nr. Hamburg	Unreg. (GPIUH)	(2)
Pseudolioceras sp.	U. Toarcian	—	Unreg. (BMNH)	(2)
Pseudolioceras lythense (Young and Bird)	U. Toarcian	Northamptonshire	C66917, −8, −9	(8)
Osperleioceras sp.	U. Toarcian	—	J30375	(2), (5)
Hildoceras sp.	L. Toarcian	—	J30359	(2)
Hildoceras sp.	L. Toarcian	—	J30356	(8)
Hildoceras sp.	L. Toarcian	—	J30352, −3, −5, −64	(2), (8)
Hildaites sp.	L. Toarcian	—	J30368	(2), (8)
Leioceras sp.	L. Aalenian	Goslar (Harz)	C4880	(2)
Stephanocerataceae				
Kosmoceras castor (Reinecke)	Callovian	—	C7932	(1)
Gulielmites sp.	Callovian	Twyford (Buckinghamshire)	C79439, −40	(8)
Cardioceras sp.	Oxfordian	—	JZ.2224	(8)
Cardioceras sp.	Oxfordian	Staffin (Skye)	C71044	(2)
Amoeboceras rosenkrantzi Spath.	U. Oxfordian	Staffin (Skye)	Unreg. (BMNH)	(2), (8)
Dimorphinites sp.	Bajocian	Yeovil (Somerset)	C52049	(8)
Perisphinctaceae				
Proplanulites sp.	Callovian	--	Unreg. (BMNH)	(8)
Binatisphinctes sp.	Callovian	Kowno (W. Russia)	C7983	(3)
Dichotomosphinctes sp.	Oxfordian	Staffin (Skye)	Unreg. (BMNH)	(3)
Crussoliceras divisum (Quenstedt)	L. Kimmeridgian	Zafarraya (Granada)	Ch.Z1.2b.1 (DPUG)	(5)
Rasenia sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C69820	(1), (3)
Rasenia sp.	L. Kimmeridgian	Horncastle (Lincolnshire)	C69831	(3), (8)
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Pararasenia sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C93899	(8)
Pavlovia sp.	Portlandian	Hartwell (Buckinghamshire)	J30355, −68, J35848, −68, −99	(5)
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Hoplites dentatus (Sowerby)	Albian	Devizes (Wiltshire)	C88627	(7)
Euhoplites sp.	U. Albian	Calais	C92747	(2)

Osperleioceras, from Toarcian black shales of southern England. All of these ammonites are fragmentary, and usually only an incomplete living chamber is preserved. Judging from phragmocone remains, these were not sediment-filled and became crushed and completely flattened during burial. Shells always display a typically iridescent appearance.

The huge collection of the Natural History Museum, London (*c.* 92000 ammonites, Mr S. Baker, pers. comm.), was reviewed during 1991 in the search for new material. Only forty-nine specimens (ranging from Pliensbachian to Campanian in age) display similar and additional features. Among them, a collection of five *Rasenia* and *Pararasenia* from the English Oxford Clay is particularly important.

Additional material housed at the Department of Stratigraphy and Palaeontology (Universidad de Granada) and at the Geologisch-Paläontologisches Institut (Universität Hamburg), including two Triassic specimens, allowed complementary observations.

For evident reasons, shell damaging analysis (e.g. SEM) were kept to a minimum; therefore, tiny structures needing high magnification are illustrated as drawings, rather than as SEM photographs. A complete faunal list, together with the kind or kinds of microsculptures recognized, is provided in Table 1.

MICROSCULPTURES

Description

Microsculptures can be differentiated into eight morphological categories. A breakdown of the specific taxa showing these categories is shown on Table 1.

(*1*) *Longitudinal wrinkles* (Pl. 1, fig. 7; Pl. 4, fig. 5). These are tiny, closely spaced, low-relief wrinkles which appear at the intercostal valleys when ribs are more or less straight, and which fade out towards both rib slopes. They are without exception longitudinal, i.e., perpendicular to ribs.

(*2*) *Adorally convergent wrinkles* (Pl. 2, figs 2–5; Pl. 3, figs 4–5; Pl. 5, fig. 4; Pl. 6, fig. 3). They are homologous to the longitudinal wrinkles, but one developed exclusively between adorally concave (all along or in part) costae. Since they always tend to be perpendicular to ribs, their orientation changes along the flank, so as to converge towards the hypothetical centre of the rib arch. Interestingly, the enigmatic feather-like ornament recorded by other authors (see Arkel *et al.* 1957, p. L92) seems to be merely a 'giant' (long wavelength) variant of this kind of wrinkle (see below).

(*3*) *Wrinkles associated with concave primary ribs* (Pl. 1, fig. 3; Pl. 4, figs 2–6). They are found at the adoral slope of specially prominent concave primary ribs. In some specimens of *Rasenia* (Pl. 4, fig. 4) they originate at the crest of the rib, and converge slightly and vanish 'downslope'.

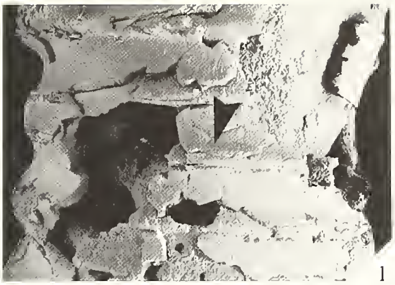
(*4*) *Dents and wrinkles on the ribs* (Pl. 1, fig. 5; Pl. 3, figs 6–7). These are more or less longitudinal features which give the ribs an irregular and deflated appearance. They are different from some low-

EXPLANATION OF PLATE 1

Figs 1–7. *Pavlovia* sp. Oxford University Museum; Hartwell, south-west of Aylesbury, Buckinghamshire; Portlandian. 1, J35857; ventral view, aperture to the top; triangular shaped kink (arrow) in an intercostal valley; × 1·4. 2, J35868; aperture to the top; periumbilical pinches; × 1·5. 3–4, J35894; oblique right and right views, aperture to the left; long radial kink at the adoral base of the third complete rib from the left, wrinkles on the concave side of primary ribs and periumbilical pinches; note also conspicuous growth lines at the adoral slope of ribs; × 2. 5–7, J35899; left, right and oblique left views; dented ribs, radial kinks, specially in 6, and longitudinal wrinkles in 7; 5–6, × 1·6; 7, × 2·2.

All specimens coated with ammonium chloride.

PLATE 1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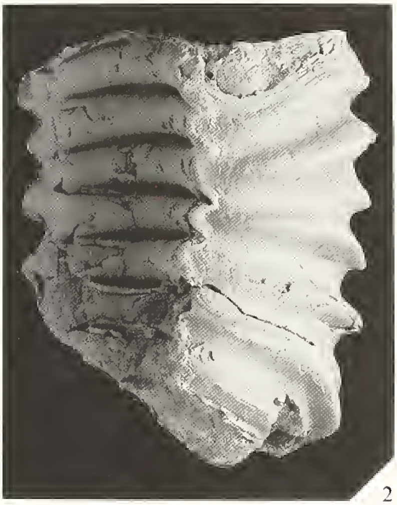
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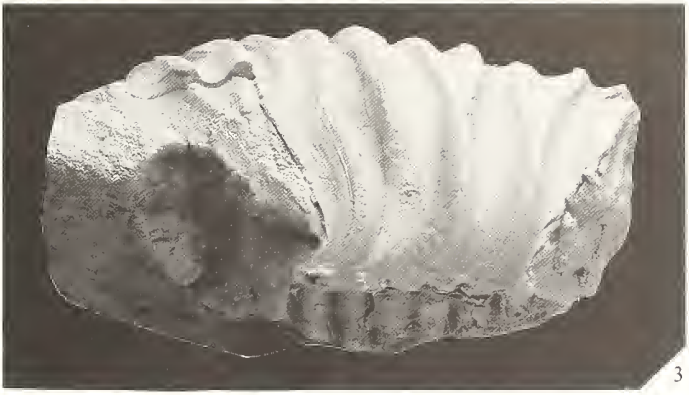
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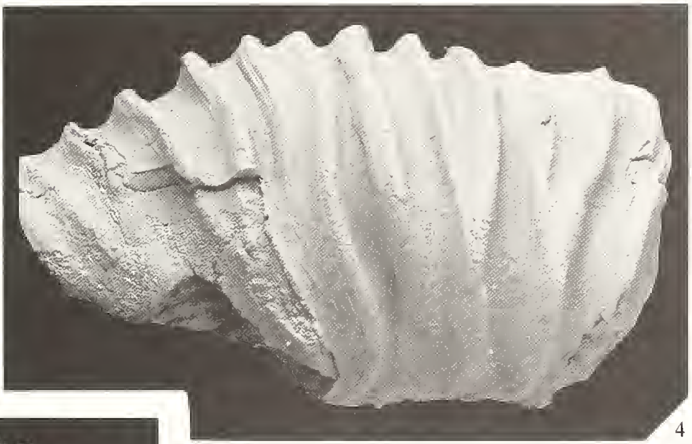
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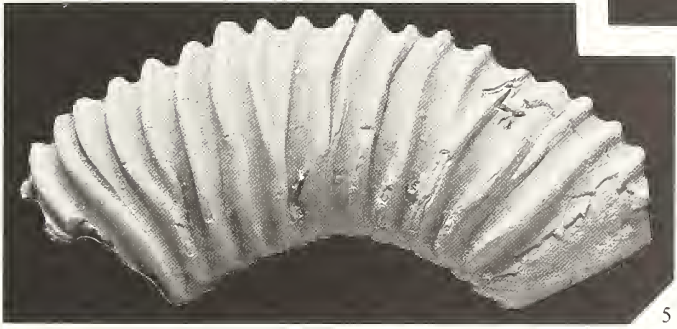
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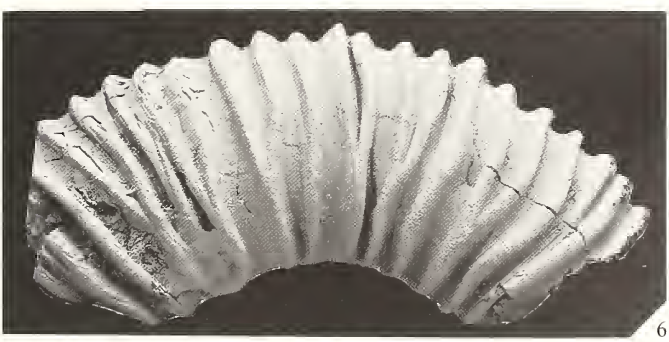
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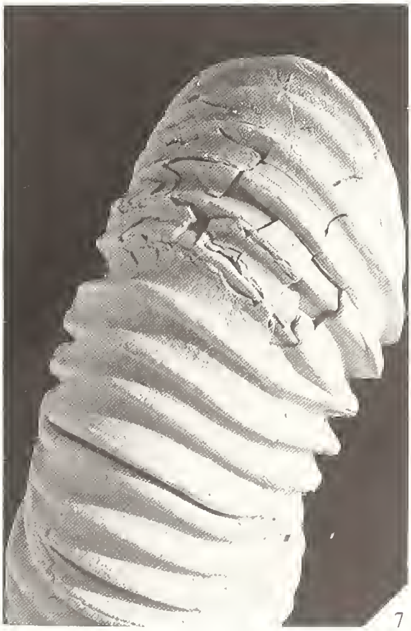
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CHECA, *Pavlovia*

relief lines crossing the rib fold (microsculpture 8), given their irregularity and their absence of homology.

(5) *Creases with kink profile* (Pl. 1, figs 1, 3–6; Pl. 3, fig. 6). They consist of intercostal, radially-elongated irregular creases with angular profile, comparable to kinks or chevron folds. They are very commonly found in *Pavlovia*, in which they can have zigzag traces in plan-view and are most commonly found at the adoral bases of ribs, specially in acute intercostal folds.

(6) *Pinches along the umbilical seam* (Pl. 1, figs 2–3). They are exclusive to the strongly-ribbed *Pavlovia* and can be described as high-relief, small folds running along the adoral slopes of the wavy intersection between the spiral tube and the ribs of the previous whorl. Judging from their aspect they seem to represent squeezing of the soft body against the ribs of the preceding whorl.

(7) *Sinuous wrinkles at the venter* (Pl. 6, figs 1–2). This feature has only been recognized in one specimen of *Hoplites dentatus*, in which a more or less continuous arrangement of narrow wrinkles adapts to the basal ventral outline of the ventrolaterally coarsened radial ribs.

(8) *Low-relief longitudinal lines or smooth longitudinal strips, and associated arcuate wrinkles* (Pl. 2, figs 2–3; Pl. 4, figs 1–2, 5–6; Pl. 5, figs 1–2, 5). This is the most common and widespread kind of feature and seems to be independent of the ribbing pattern. It consists usually of narrow longitudinal (spiral) lines with slightly negative relief which are restricted, with some exceptions, to the intercostal valleys. These lines can have discontinuous tracings in the sense that they disappear and reappear intermittently when crossing either ribs or their valleys. This is the only microsculpture displaying homology over consecutive ribs. In some instances (in *Gulielmites*, *Baculites* and *Androgynoceras*, for example) low-relief lines are substituted by smooth bands. Sets of wrinkles may be found associated with low-relief lines or smooth bands. They are adorally-convex or chevron-like in plan view and are concentrically arranged, as if they hung from consecutive low-relief lines, in a 'drapery-like' fashion. In other instances, wrinkles are absent.

Interpretation

The existence of a free periostracum. In general, all of the observed features, except for type (8), seem to be products of non-fragile deformation of a flexible material. Therefore, none of them will have resulted from cracking of the shell during burial. Some cracks of taphonomic origin (Pl. 3, fig. 5) can be easily recognized by their fragile style. Microsculptures are also quite different from repaired injuries (e.g. see Hölder 1955, 1970; Guex 1967, 1968; Bayer 1970; Lehmann 1981; Landman and Waage 1986).

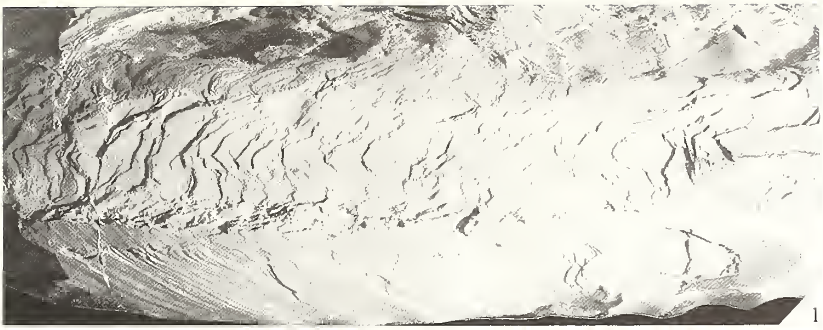
EXPLANATION OF PLATE 2

Figs 1–3. *Hildaites* sp. Oxford University Museum, J30368; locality unknown; lower Toarcian. 1, ventral view, aperture to the left; nacreous lamellae plunging apically; × 1·5. 2–3, right view; adorally convergent wrinkles at the upper flank and low relief longitudinal lines and conspicuous associated wrinkles; note also non-congruence of ribs and growth lines; numbers in 2 are the angles formed by growth lines at the lateral sinus (see text); 3 is a composite photograph; 2, × 1·5; 3, × 1·7.

Figs 4–5. *Hildoceras* sp. Oxford University Museum; locality unknown; lower Toarcian. 4, J30359; oblique left view, adorally convergent wrinkles; × 1·9. 5, J30353; left view, complexly arranged adorally convergent wrinkles; × 1·8.

All specimens coated with ammonium chloride.

PLATE 2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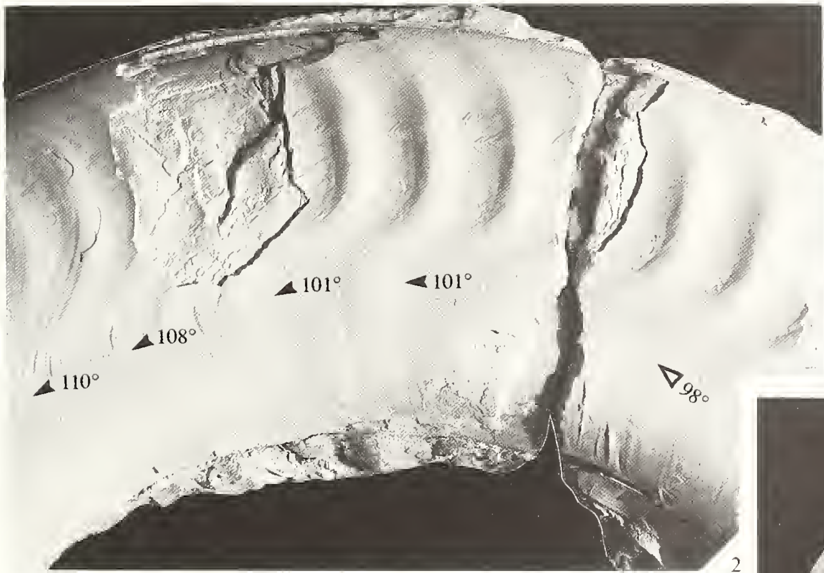

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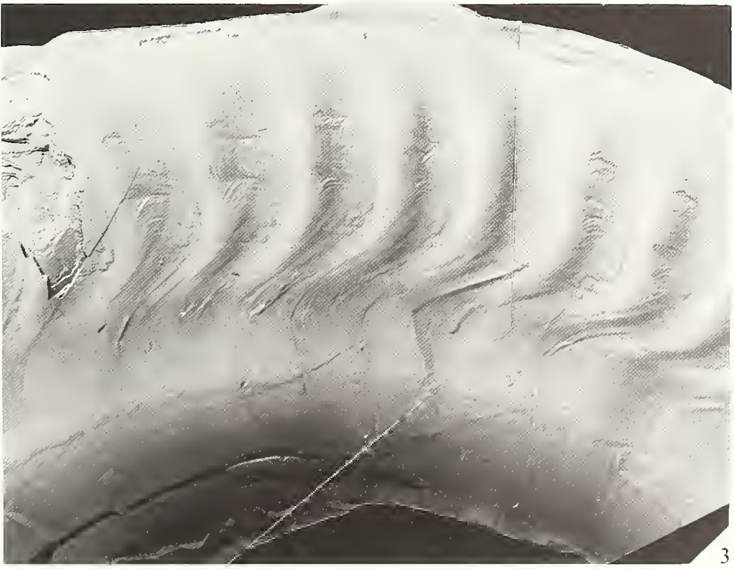
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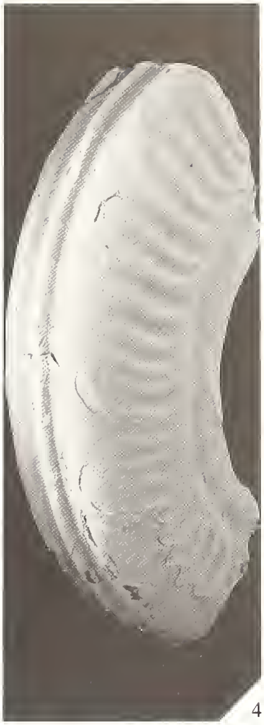
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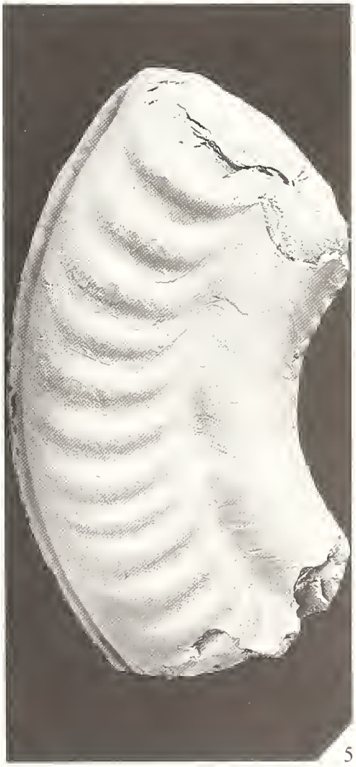
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CHECA, *Hildites*, *Hildoceras*

Given their ductile appearance, the most likely hypothesis is that the many rib-associated microsculptures occurred in life, in a non-calcified shell, that is, after secretion of the organic shell (periostracum) by the mantle lobe and before, or immediately after, the periostracum began to calcify. This is the so-called free periostracum. In present-day molluscs the free periostracum is a thin, pliable, fibrous layer which bears the growth lines and serves as a matrix for the deposition of calcium carbonate crystals. The fluid-filled extrapallial space separates the periostracum from the soft body. Calcification begins some way back after the periostracum is extruded by the mantle margins (periostracal groove; see Saleuddin and Petit 1983 and Text-fig. 3). Although Miller *et al.* (1957) supposed that the ammonite shell must have included a periostracal layer, its existence had not been recognized in previous studies on the shell structure (e.g. see Howarth 1975; Kulicki 1979; Birkelund 1980). This is, to my knowledge, the first evidence of a widespread free periostracum stage in ammonoids. Therefore, there are no reasons to assume different modes of calcification in ammonites and in present-day molluscs. The fact that growth lines (and, hence, the periostracum) were formed prior to wrinkling is evident, since growth lines, which were discontinuities on the periostracum, served usually as nucleation lines for wrinkles of types (1), (2) and (5) (Pl. 2, figs 2–3, 5; Pl. 6, fig. 3). In other instances wrinkles of type (2) only span the space between consecutive growth lines (Pl. 2, figs 2–3; Pl. 5, fig. 1; Pl. 6, fig. 3). A casual transversal break in the shell of a *Pavlovia* (Text-fig. 1A) crosses a radial kink and an associated small radial break; it can be appreciated how both features are immediately mitigated inwards of the shell, so that they had to be formed when the shell was less than one-twentieth of its final thickness.

Compressional microsculptures. In Recent molluscs the free periostracum is usually a flexible thin film. Although I have not found detailed studies of its mechanical properties, independently of its degree of tanning, the periostracum can be classified as a viscoelastic material, such as, for example, insect cuticle. Viscoelastic materials increasingly deform under tensile or compressive stress; once the stress is removed, recovery is also gradual, so that any measurement of strain is time-dependent (see Wainwright *et al.* 1976, fig. 2.12).

With the exception of type (8), all the other microsculptures are very similar in morphology to compressional features. In fact, types (5) and (7) are typical features resulting from Brazier-type buckling. This is a short-wave mode of buckling, typical of thin-walled cylinders, which are compressed axially (see Gordon 1978); in these conditions, a crease or crumple will develop when the stress in the skin is equivalent to:

$$\tfrac{1}{4}E\frac{t}{r},$$

being: E, Young's modulus, t, wall thickness and r, tube radius. We should remember that Young's modulus is the ratio of stress to strain and is constant for linearly elastic (Hookean) materials. The

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EXPLANATION OF PLATE 3

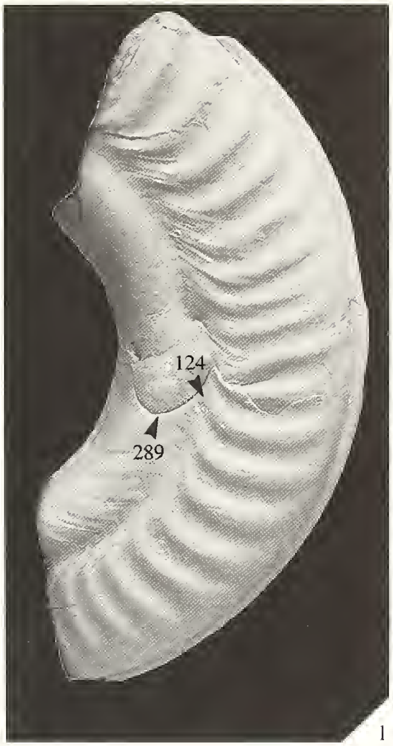
Figs 1–3. *Hildoceras* sp. Oxford University Museum, J30364; locality unknown; lower Toarcian; right, ventral and left views; repaired predatory injury, numbers refer to thickness (in μm) of the abandoned shell edge at different sites; × 1·5.

Figs. 4–5. *Osperleioceras* sp. Oxford University Museum, J30375; locality unknown; upper Toarcian; left view; adorally convergent wrinkles; 4, × 3; 5, × 1·3.

Fig. 6. *Peronoceras* sp. Oxford University Museum, J31943; locality unknown; lower Toarcian; right view; dented ribs, longitudinal wrinkles; note also the 'deflated' appearance of the shell; × 1·8.

Fig. 7. Dactylioceratidae sp. Departamento de Estratigrafía y Paleontología, Universidad de Granada, Ch.S$_1$; locality unknown; Toarcian; ventrolateral right view; dented ribs; × 5·5.

All specimens coated with ammonium chloride.



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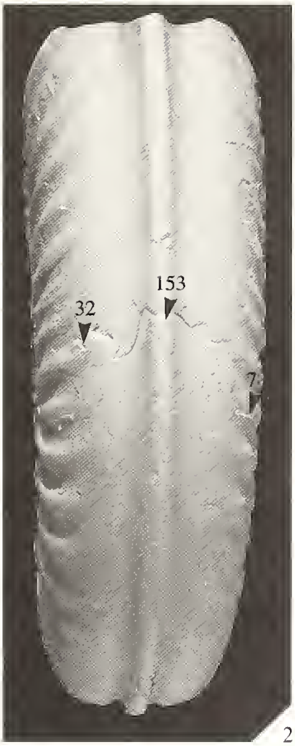

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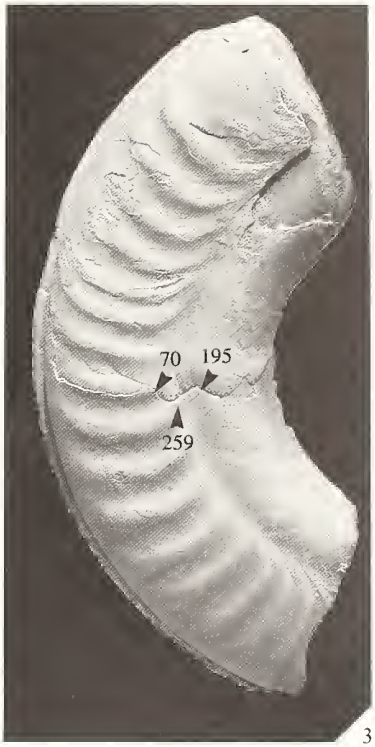

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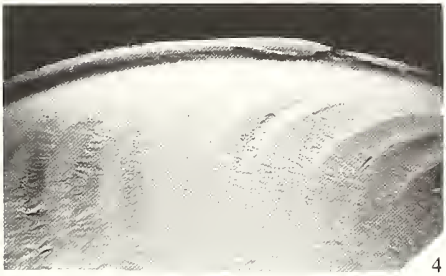

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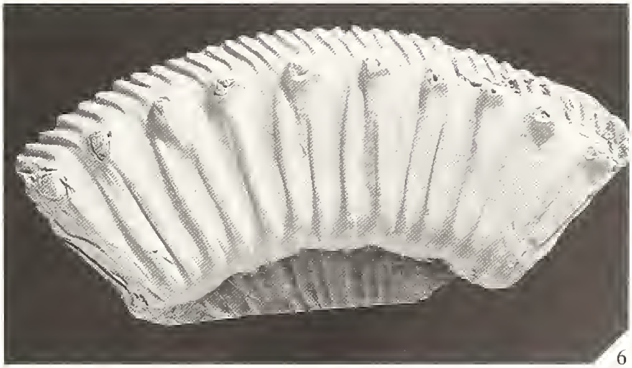

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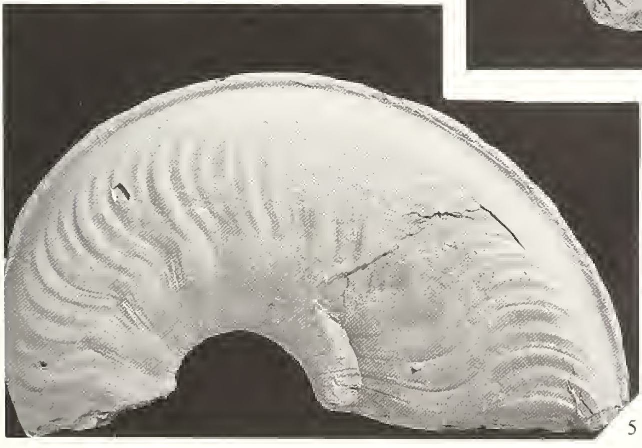

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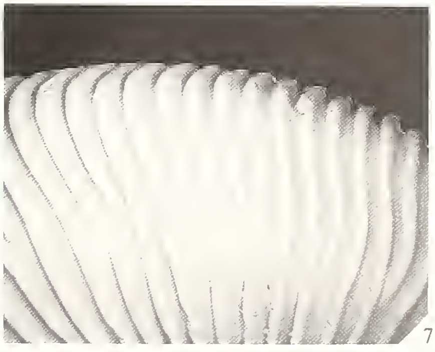

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CHECA, *Hildoceras*, *Osperleioceras*, *Peronoceras* probability of Brazier buckling is thus greater as the wall thins proportionally to tube radius and for low-stiffness (low E) materials. Therefore, microsculptures (5) and (7) could well have developed on a thin, non- to incipiently calcified periostracum, under compressive stress. The fact that in some specimens of *Pavlovia* some kinks developed into small, inverse fault-like cracks (Text-fig. 1A) can be explained by invoking a slightly calcified periostracum; this would be more likely to crack (that is, it behaved like a linearly elastic material) than if it was not calcified at all. Since the periostracum usually calcifies progressively as it leaves the apertural edge, these differences in calcification may also imply distance to the mouth.

Type (4) dents are typical of small defects acquired during the folding process. These can be demonstrated by attempting to fold a large piece of paper on a planar surface by pushing at both ends, which result in several wrinkles parallel to the stress direction rather than smoother folds.

Longitudinal (1) and adorally convergent wrinkles (2) can also be explained in a compressional context if some contraction occurred along the intercostal valley, transversal to the main compressional stress. Just imagine the uncalcified shell as a more or less smooth spiral tube which contracted longitudinally, so that a series of anticlines (ribs) and synclines (valleys) formed. The cross-sectional perimeter then enlarged along the rib height and diminished along the valleys; circumferential shortening within the intercostal valleys must be compensated for by wrinkling the periostracum. Adorally convergent wrinkles represented the same situation for concave ribs. Microsculptures (1) and (2) can be easily reproduced in the laboratory by adapting a thin plastic film to a surface modelled like ribbed ammonite flanks. Both in the cases of radial and concave ribs adaption (i.e. compression) of the film gave rise to the expected longitudinal (Text-fig. 2A) and adorally convergent wrinkles (Text-fig. 2B) respectively. In plasticine models wrinkles are much wider than in ammonites, since the plastic film is surely thicker than the ammonite periostracum was. According to Biot *et al.* (1961), when a layer (of viscosity μ_1) embedded in a less viscous medium (μ_2) is folded by lateral contraction, the dominant wavelength of the folds is given by:

$$2\pi t \sqrt[3]{\frac{\mu_1}{6\mu_2}},$$

t being the thickness of the layer. This formula could partly hold for ammonite periostracum, lined internally by the soft body through the extrapallial space. The whole pattern of wrinkles obtained experimentally is also much more irregular than ammonitic patterns, probably because the existence of longitudinal attachment lines of the soft body to the periostracum (see below) contributed to an ordered folding and wrinkling.

The ammonitic periostracum was also much less intensively wrinkled than expected in plasticine experiments, given the foreseeable radial shortening along the valleys between ribs (compared with laboratory models). This implies that the periostracum was also probably inflated elastically at the ribs, which agrees with its supposed viscoelastic behaviour.

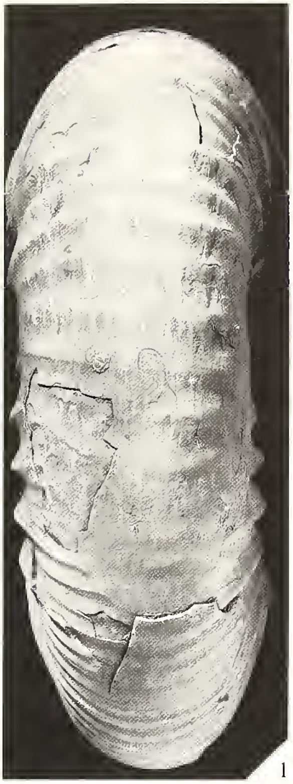
EXPLANATION OF PLATE 4

Figs 1–2. *Pararasenia* sp. Natural History Museum, C93899; Market Rasen, Lincolnshire; Lower Kimmeridgian; ventral and left views; primary ribs disappear after the injury and secondary ribs become smooth and widely spaced; note also high-relief longitudinal lines; ×1.

Figs 3–6. *Rasenia* sp. Natural History Museum. 3, C69831; Horncastle, Lincolnshire; Lower Kimmeridgian; left view; more concave ribs display better developed wrinkles; ×1. 4, C69820; Market Rasen, Lincolnshire; Lower Kimmeridgian; left view; wrinkles associated with concave primary ribs; ×5. 5, C70514; Market Rasen, Lincolnshire; Lower Kimmeridgian; right view; wrinkles associated with concave primary ribs, longitudinal wrinkles in intercostal valleys and low-relief longitudinal lines at rib heights; ×2·5. 6, C69832; Market Rasen, Lincolnshire; Lower Kimmeridgian; right view; wrinkles on concave primary ribs and low-relief longitudinal lines with associated wrinkles; ×1.

All specimens coated with ammonium chloride.

PLATE 4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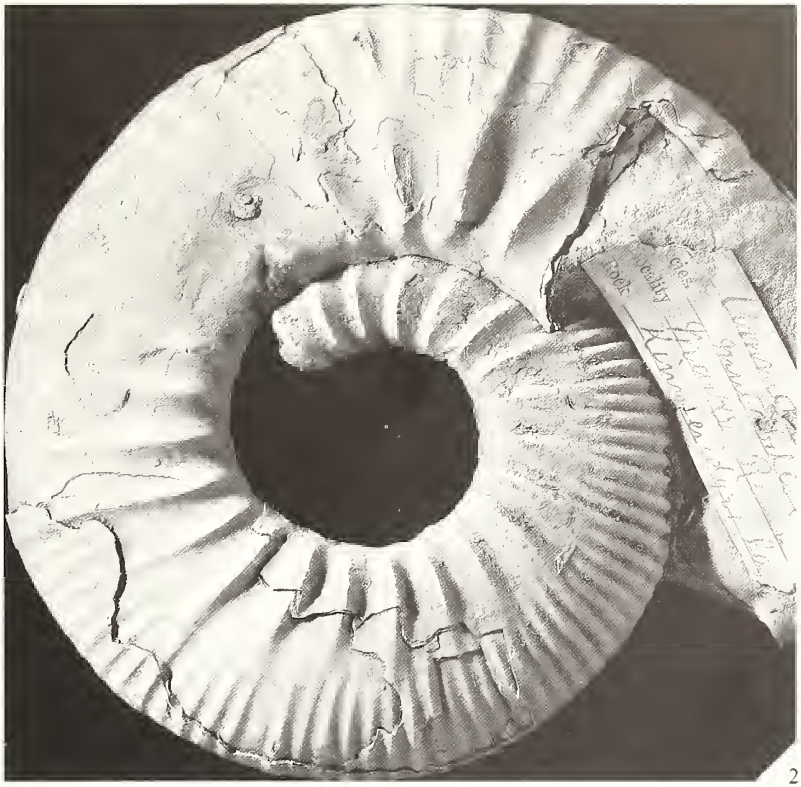
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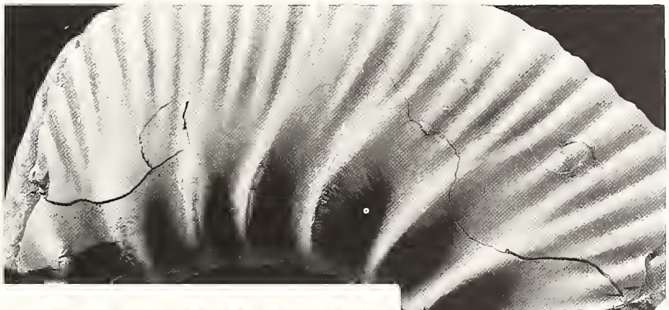
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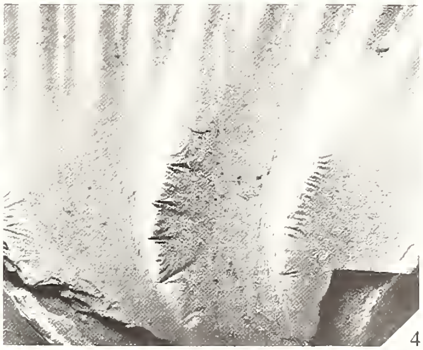
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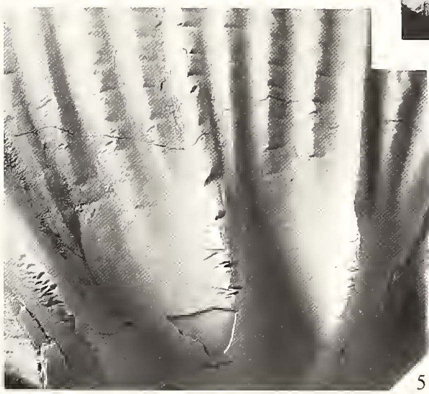
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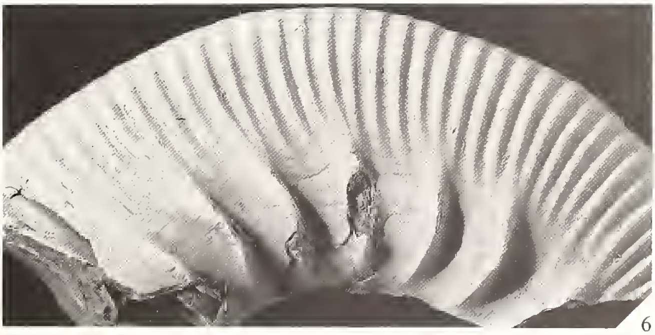
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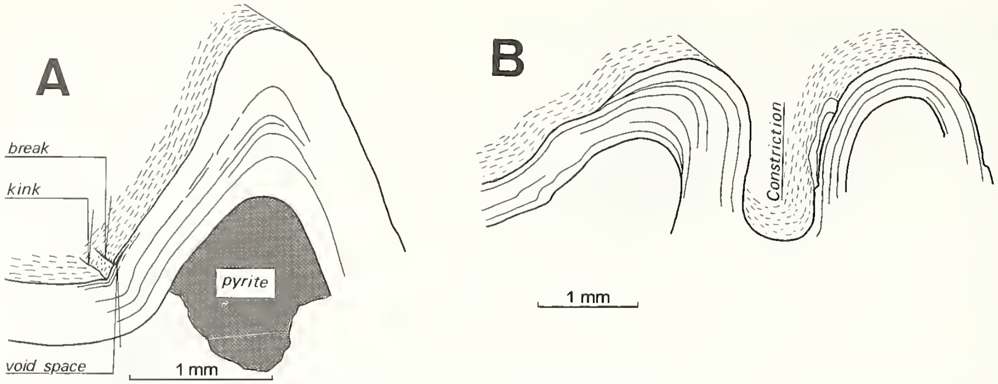
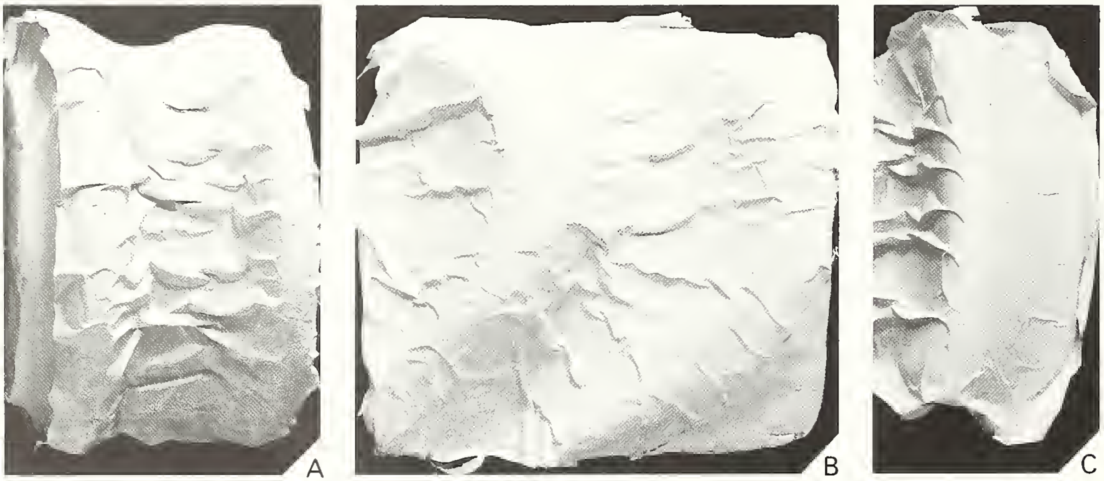
CHECA, *Pararasenia*, *Rasenia*



TEXT-FIG. 1. Camera lucida drawings of shell sections of *Pavlovia* sp., from specimens at the Oxford University Museum; Hartwell, south-west of Aylesbury, Buckinghamshire; Portlandian. A, J35891; radial kink and associated break developed at the base of the adoral slope of a rib; deformation was restricted to the outermost shell and the more internally secreted shell was not folded, although it accommodated to the previous kink. B, J35883; internal distribution of lamellae; after the constriction, shell lamellae fade out at the subsequent rib and are replaced by new lamellae growing under the rib (see also Text-fig. 4). Growth direction is to the left in both cases.



TEXT-FIG. 2. Laboratory reproduction of selected microsculptures; ×0·75. A, intercostal longitudinal wrinkles, microsculpture (1). B, adorally convergent wrinkles, microsculpture (2). C, wrinkles developed at the concavity of primary ribs, microsculpture (3). In A and B a plastic film was adapted to a previously modelled surface; in C the plastic film was attached onto a straight rib which was subsequently curved.

In the reticulated surface of *Amaltheus* shells (Pl. 5, fig. 1), wrinkles appear along the diagonals of quadrangles formed by the intersection of low-relief longitudinal lines (8) and growth lines. These are interpreted as adorally convergent wrinkles modified by the intersection with a grid originally formed on the periostracum.

Wrinkles associated with concave primary ribs (3) are also compression features developed in a pliable skin when a previous fold is folded again along an axis transversal to the previous folding axis, but contained in the same axial plane. Just adapt a plastic sheet to a folded surface and try now to curve the hinge of the fold. Wrinkles vanishing outwards from the fold will develop in the concave slope (Text-fig. 2C). This agrees with the fact that in some specimens of *Rasenia* in which primary ribs display different degrees of concavity, wrinkles gain in development with increasing concavity of the primary rib (Pl. 4, figs 3–4).

Periumbilical nips (6), even though compressional, are different from the above features in that they seem to have been developed on a purely elastic material. In two specimens of *Pavlovia* (Pl. 1, figs 2–3), periumbilical nips sometimes continue backwards into the primary ribs through tiny ridges. In these cases features of types (3) and (6) may have resulted from the same retraction episode of the soft body; in this way, no backwards motion actually occurred at the umbilical seam, in which the soft body became adpressed against the dorsum, leading to periumbilical nips. The fact that periumbilical nips seem to have developed in a highly elastic material may imply closeness to the apertural edge. Retraction took place progressively away from this seam, which made the primary ribs arch at the same time they were formed (Text-fig. 6C). Another area involved in this process was the dorsum. Attachment of the soft body to the dorsal area took place probably through the wrinkle layer (Walliser 1970; Bayer 1974; Doguzhaeva and Mutvei 1986).

Longitudinal lines and associated arcuate wrinkles. This feature is similar to the ones described above, in that it was also developed in a non-calcified periostracum in an apertural or near-apertural position (since no breaks are associated). The 'drapery-like' appearance of these structures provides a very suggestive clue to their origin. The most immediate explanation is that low-relief lines or smooth longitudinal bands were attachment lines of the periostracum to the soft body, whereas the periostracum between them was unattached and free to bulge and wrinkle by radial contraction along the intercostal valley (as in hildoceratins; see below). In a large specimen of *Hildaites*, wrinkles fade out with the disappearance of ribs towards the end of the living chamber (Pl. 2, fig. 2), which gives evidence of their relation to periostracum compression and bulging. The fact that homologous lines appear over several consecutive ribs implies that they are not casual effects; they were probably thin elongated tissular connections which, with growth, left a spiral trace on the periostracum (and, hence, on the shell).

When chevron wrinkles are specially well developed (Pl. 2, figs 2–3) it can clearly be appreciated how they are distributed into two sets forming an angle of some 90°, that is at ±45° of the foreseeable longitudinal shear stresses developed on the uncalcified periostracum (Text-fig. 3). Creases arranged in this fashion are the result of tensile and compressive stresses in directions at 45° to the plane of shearing, forming what is called by engineers a 'Wagner tension field' (Gordon 1978). The resultant arrangement of wrinkles is comparable to what is known as 'drape' in the textile trade. It is dependent on the shear modulus or modulus of rigidity G of the material, which is the ratio of shear stress to shear strain and represents the stiffness of the material in shear. On the whole, the higher the shear modulus of a material, the greater its tendency to creasing. The fact that the best developed wrinkles have been found in the big specimen of *Hildaites* implies that probably the periostracum in this specimen displayed an unusually high rigidity (high G). A likely hypothesis is that periostracum thickness (and hence stiffness) increased with size of the ammonite, so that at great diameters it tended to crease by shear. Smaller-sized individuals of *Hildoceras* do not display arcuate wrinkles, which can be related to the fact that their periostracum was thin enough to get a closer and more flexible fit to the soft body shape when folding occurred.

In some ammonites (e.g. *Rasenia*), low relief lines are well developed over the rib heights (which have a general appearance of deflation) and absent in the valleys (Pl. 4, fig. 5). In other cases they appear exclusively at the valleys, whereas ribs are neatly inflated (Pl. 2, figs 2–3). This implies that differential attachment could have taken place at different sites in different ammonites.

Analogous structures have been reported in acrotretoid brachiopods by Williams and Holmer (1992), who called these drapes (arcuate wrinkles) and nick points (lines of union of wrinkles). They supposed that nick points coincided with insertions of setal muscles, so that at these sites the forward growth of the shell was reduced compared to drapes. Evidently, this origin is unlikely for ammonites.

SHELL SECRETION MODE AND THE CONSTRUCTIONAL MORPHOLOGY OF APERTURES

Periodicity of rib formation

The above data imply that ribs were compressional features in the most strict sense. Complementary data about this mode of construction come from the study of other features which, in general, suggest that ribs were constructed in independent cycles of growth and compression.

In some *Pavlovia*, radially elongated kinks are found at the adoral base of each rib, specially at the ventral area (Pl. 1, figs 3–7; Text-fig. 1A). Conspicuous growth lines are also developed at this adoral slope. The basis of this slope could have constituted at some moment the boundary between a slightly calcified and a non-calcified shell; this discontinuity within the material was probably the most appropriate site for kink formation, since stresses could not have been easily transferred apicalwards of the shell. Inverse local kinks were also detected in one *Oistoceras fibulinum* (Pl. 5, fig. 5) at the apical slope of ribs, coinciding with marked growth lines.

Megastriations (*mégastries*) were defined by Bucher and Guex (1990) in some Triassic ammonoids as sites of periodic shell resorption. Interestingly, they invariably follow the apical limit of ribs, except for some intercalary and simple ribs (Bucher and Guex 1990, figs 3, 6). Therefore, the compressional mode of rib formation could have been present already in Triassic ammonoids, even though associated microsculptures have not yet been recognized.

A large specimen of *Hildaites* (Pl. 2, figs 2–3) displays spaced, low-relief radial lines at the lower flank; at two-fifths of the flank height they become retroverse, thus forming a lateral sinus, and develop into conspicuous growth lines which run upwards to join the ribs. These lines and their associated striations are much more developed and quite distinct from usual growth lines, and seem to correspond to growth halts. They tend to disappear towards the end of the body chamber, coinciding with mature weakening of the ribs. I have measured the apical angle formed by these striations and their backwards projections along the specimen and found it to increase significantly (by some 10°) with rib weakening towards the aperture. Four values (out of thirty-three) for this angle are provided in Plate 2, figure 2. This is consistent with the fact that the periostracum was differentially retracted and folded at the ribs; local retraction made the retroverse branch of striations rotate clockwise, such as they appear in Plate 2, figures 2–3, approaching the lower, radial branch and narrowing the angle between them. Since ribs (and hence retraction) tended to disappear towards the final mouth, the original, high-angled traces remained undeformed here.

EXPLANATION OF PLATE 5

Fig. 1. *Amaltheus stokesi* (Sowerby). Natural History Museum, C10380; Stroud, Gloucestershire; Pliensbachian (Margaritatus Zone); left view; reticulated surface of the shell with diagonal wrinkles which are interpreted as a variant of adorally convergent wrinkles; ×2.

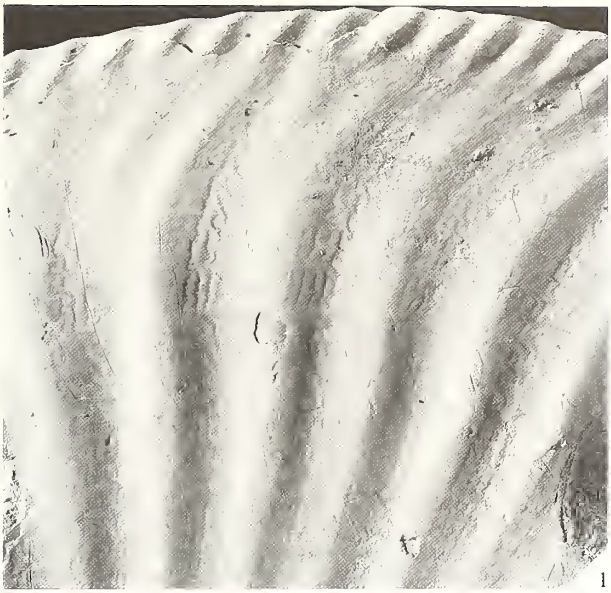
Fig. 2. *Baculites chicoensis* Reeside. Natural History Museum, C53070; Nanaimo, Vancouver Island; Campanian; left view; sets of adorally convex wrinkles with interspersed smooth bands on an intermediate shell layer; note the extremely wrinkled appearance of the outer shell surface preserved at the left bottom; ×1·5.

Fig. 3. *Cardioceras* sp. Natural History Museum, C71044; Trotternish, Staffin, Isle of Skye; Oxfordian; right view; growth lines cross ribs at the upper flank, near the ventral keel; ×4.

Fig. 4. *Tragophylloceras boblayei* (d'Orbigny). Natural History Museum, C28215; Cheltenham, Gloucestershire; Pliensbachian (Ibex Zone); left view; thin adorally convergent wrinkles; ×1·5.

Fig. 5. *Oistoceras figulinum* (Simpson). Natural History Museum, C73534; Kirton in Lindsay, Lincolnshire; Pliensbachian (Davoei Zone); ventral view, aperture to the top; well-marked growth lines, sometimes developing locally into inverse kinks, at the apical slope of ribs and high-relief longitudinal lines; ×2.

All specimens coated with ammonium chloride.



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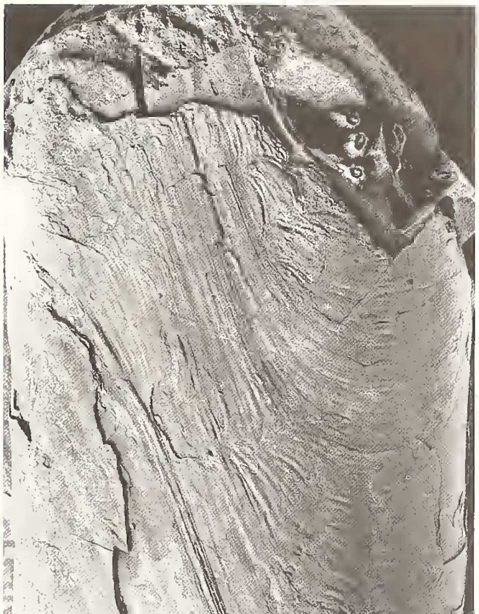

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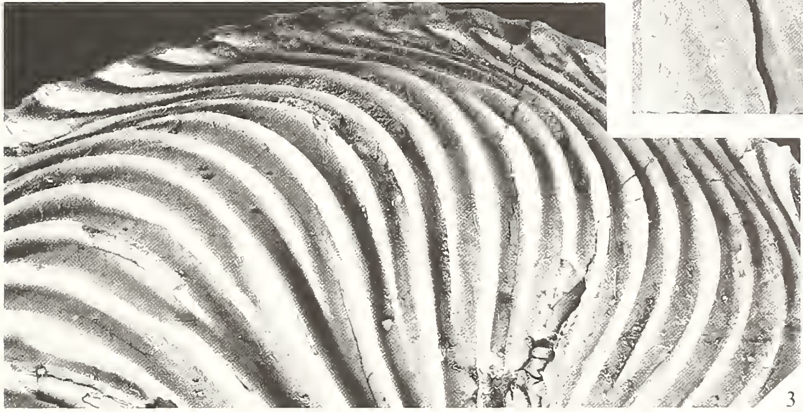

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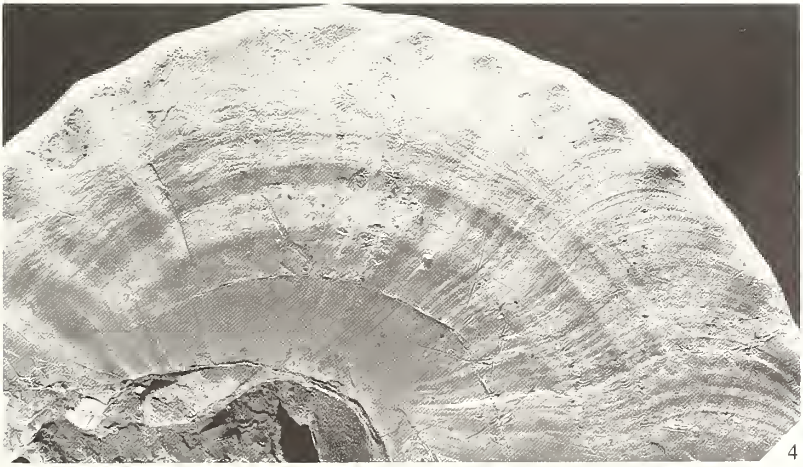

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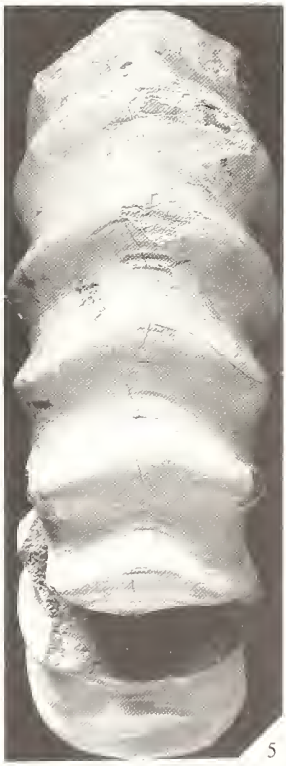

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CHECA, *Amaltheus*, *Baculites*, *Cardioceras*, *Tragophylloceras*, *Oistoceras*

Modes of calcification

The model presented here implies that the periostracum was, to some extent, secreted intermittently and that its calcification must have been intermittent. Accordingly, I have searched for evidence of internal cyclicity within the shell. The only data in this respect are provided by Bucher and Guex (1990), who found megastriations to be the external intersection of two superimposed shell layers. Data gathered from the material studied show that this figure is general, although in detail two modes of timing in shell secretion can be distinguished, according to whether constrictions are present or not.

Non-constricted forms. In *Hildaites* and *Hildoceras* there is evidence that the apertural area took the form of an acute wedge in longitudinal cross-section, and therefore, the thinnest part of the shell at any moment of growth (except, possibly, for the final aperture). In the large specimen of *Hildaites*, the outer (nacreous) shell had been severely eroded at several places revealing the internal distribution into lamellae (Pl. 2, fig. 1). These are clearly imbricated, plunging apically, and each lamella apparently departs from one growth line. Kulicki (1979, pl. 47, fig. 7) found similarly arranged discontinuities within the shell of the Callovian genus *Quenstedtoceras*. In one *Hildoceras* (Pl. 3, figs 1–3) the aperture was severely injured by predation before maturity and the old damaged aperture remained exposed since the newly produced shell initiated under the old one. Shell thickness was measured at several points of the old aperture using a binocular microscope, attached to a Sony Magnescale unit for measuring stage displacement, with a precision of 1 μm. Measurements revealed an increasing shell thickness from the very edge apicalwards. I should point out the extreme apertural thinness at the moment of the injury. Other small injuries in *Hildaites* (Pl. 2, fig. 2) and *Hildoceras* (Pl. 2, fig. 4) reveal the same pattern.

Constricted forms. In specimens of the genus *Pavlovia*, constrictions are rather numerous and they are typically developed every two or three complete primary ribs (plus the corresponding secondary and, eventually, intercalary ribs). The secretion pattern here is very different from that of hildoceratins, since the adoral slope of each rib formed immediately after the constriction marked the end of a shell secretion cycle. Here, the well marked surficial growth lines continue into the shell as lamellae extending backwards and wedging out under the rib, limiting the previous constriction adorally (Text-figs 1B, 4). Therefore the sector occupied by two successive constrictions corresponds to cycles of shell secretion. In *Pavlovia*, then, after the complete corrugated margin was thickened at the last-formed constriction, the body advanced rapidly while secreting a (slightly folded?) periostracum, which at this stage was only slightly, if at all, calcified. Repeated folding of the periostracum led to new ribs and growth stopped somewhat beyond the last calcified shell, when a new constriction was to be formed (Text-fig 6B). The animal secreted several parallel lamellae under the new shell until a thickened, fully calcified shell and aperture (constriction and subsequent rib) were obtained, when a new cycle was initiated. Therefore, the mode of shell secretion was episodic,

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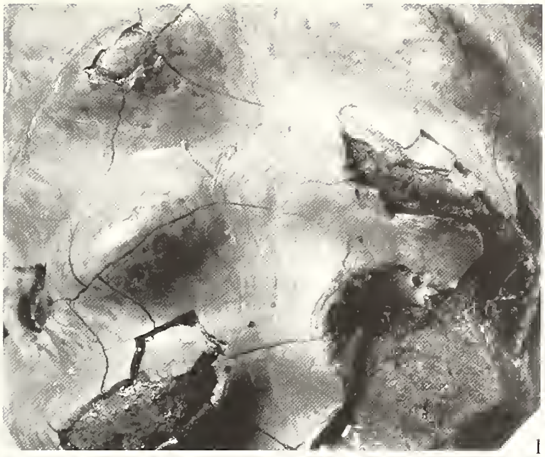
EXPLANATION OF PLATE 6

Figs 1–2. *Hoplites dentatus* (Sowerby). Natural History Museum, C88627; Devizes, Wiltshire; Albian; ventral view, aperture to the top; ventral sinuous wrinkles at the bases of ventrolateral tubercles; ×3.

Fig. 3. *Placenticeras umkwelanensis* Klinger. Natural History Museum, C93898; Mfolozi and Umkwelane Hill area, Zululand; Coniacian; left view; typical feather-like ornament; ×4.

Fig. 4. Arietitidae sp. Natural History Museum, C41785; Timsbury, near Radstock; Lower Lias; right view; growth lines between growth increments appear in low-relief at the intercostal valleys (light areas) and, usually, in high-relief at the ribs (dark bands); ×3.

All specimens uncoated.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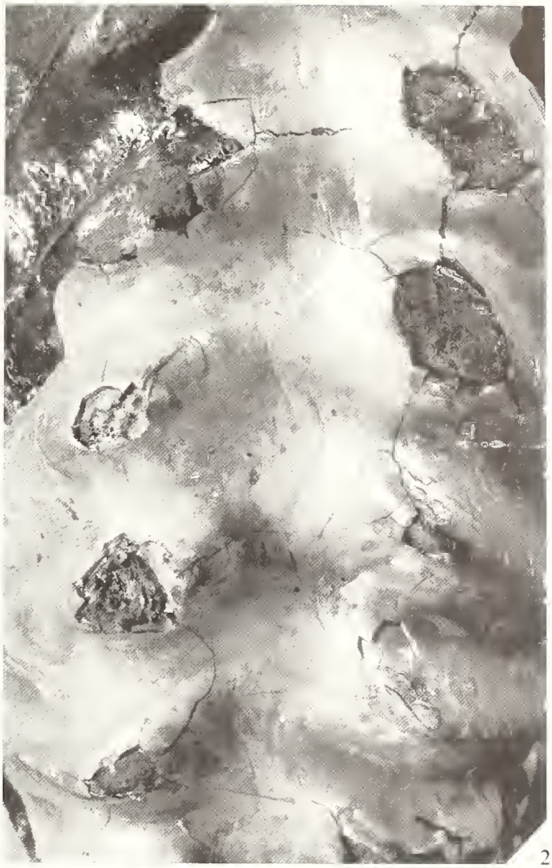
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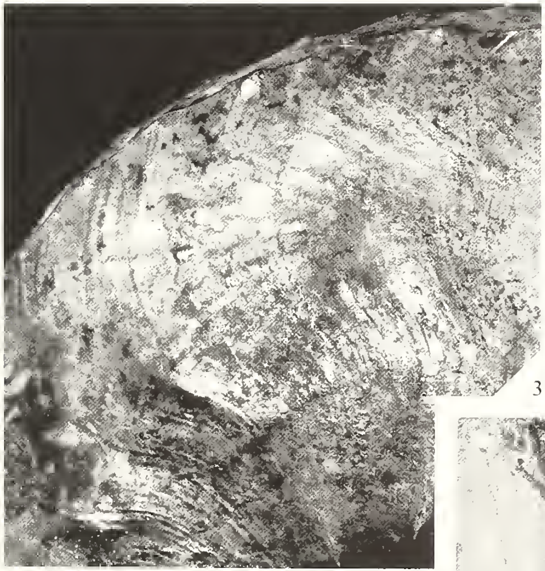
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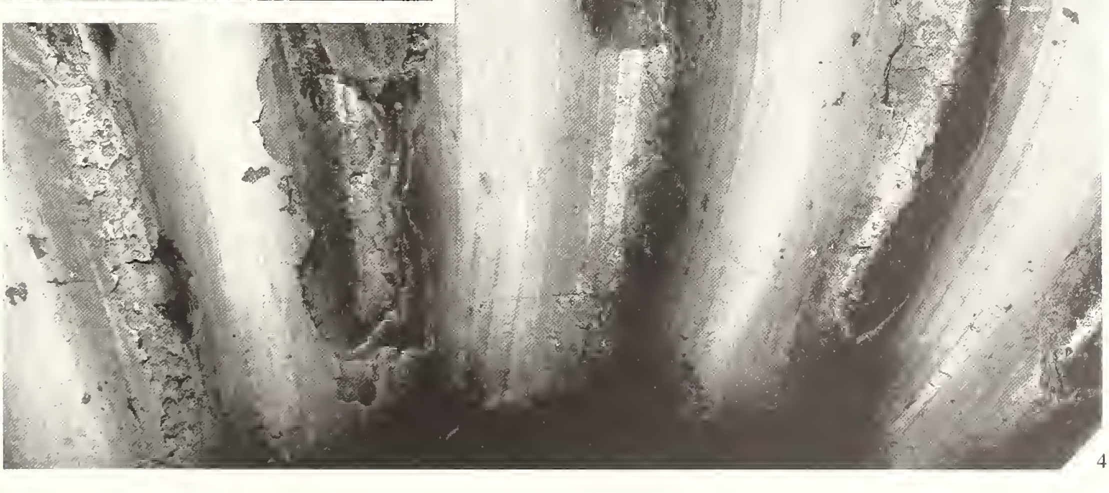
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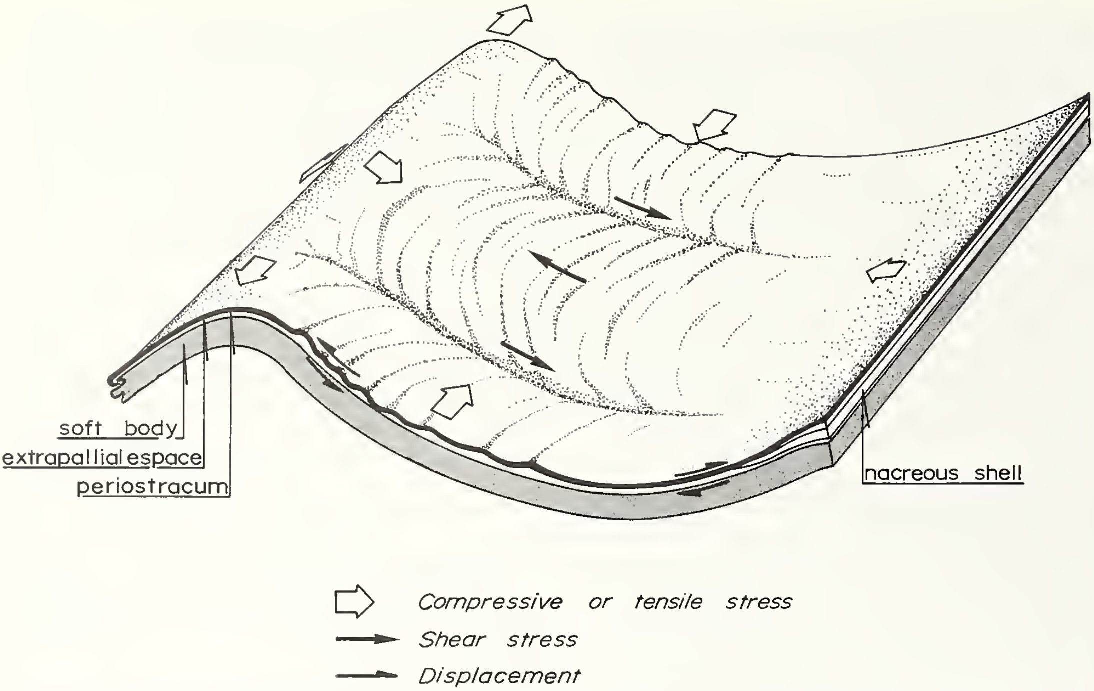
CHECA, *Hoplites*, *Placenticeras*

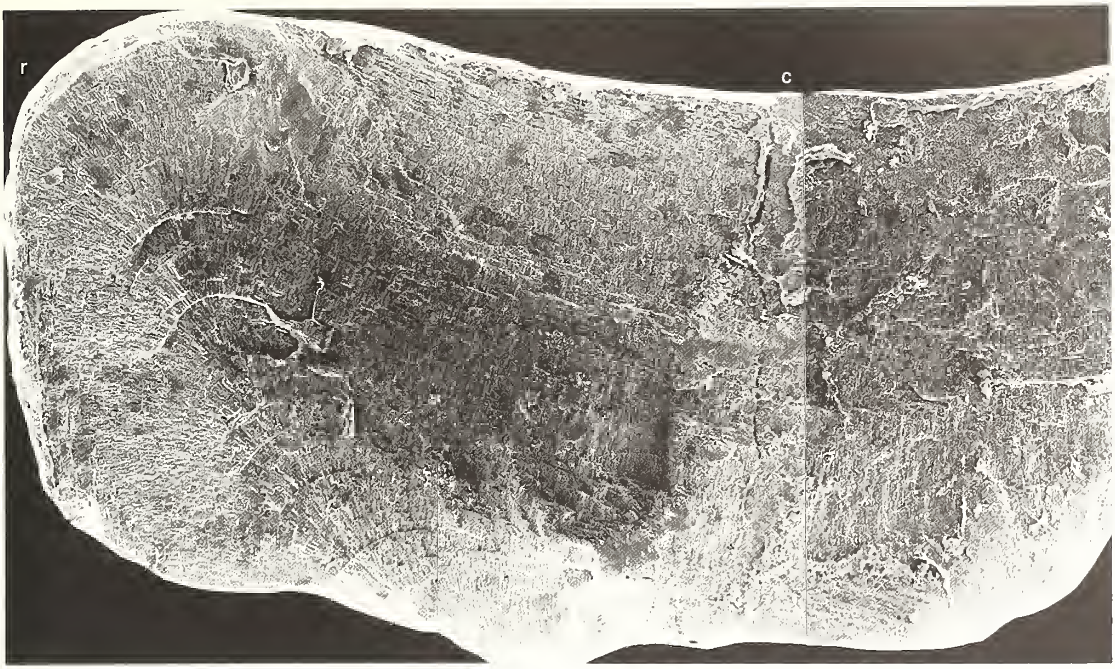


TEXT-FIG. 3. Inferred distribution of stresses during the process of contraction and folding of the uncalcified periostracum of ribbed ammonites. Tensile radial and longitudinal stresses developed at the rib, whereas the intercostal valley was compressed radially (if radial shortening occurred) and longitudinally. Shear stresses arose between longitudinal lines of attachment (in low-relief) and intermediate areas, with the formation of adorally convex wrinkles. Formation of sinusoids also led to minor displacements between periostracum and soft body. Growth direction is to the left. Although mainly based on *Hildaites* (see Pl. 2, figs 2–3), the figure is intended to represent a general case.

in much the same way as that described by Linsley and Javidpour (1980) in some gastropod families in which lamellae between constrictions are similarly arranged. Although I only describe the case of *Pavlovia*, this pattern could probably be applied to many other constriction-bearing shells. Future work is needed in this respect.

Apertures, ribs and constriction: functional aspects

Both for hildoceratids and pavloviids the creation of a thin, scarcely resistant shell could have been adaptive. An easy-to-tear aperture would have allowed the animal to get free from benthic predators gripping the aperture during the subjugation phase (e.g. decapod crustaceans; see Lehmann 1981; Ward 1981) with minimal shell losses. Then the ammonite was able to swim out of the reach of the predator. It should be stressed that four out of seven specimens of Hildoceratinae (57 per cent) displayed repaired apertures. Note that these features were not transmitted to the mould. This mechanism makes sense only if the ammonite also had the ability to retract more or less deeply inside the shell; this could have been the case with ammonites, judging by the internal position of the mouth complex in *Arnioceras* (Lehmann 1971) and, coincidentally, *Hildaites* (Lehmann and Weitschat 1973). A similar attitude of passive defence was supposed by Lehmann and Kulicki (1990, fig. 2) from the study of aptychi. As soon as hildoceratids reached maturity and

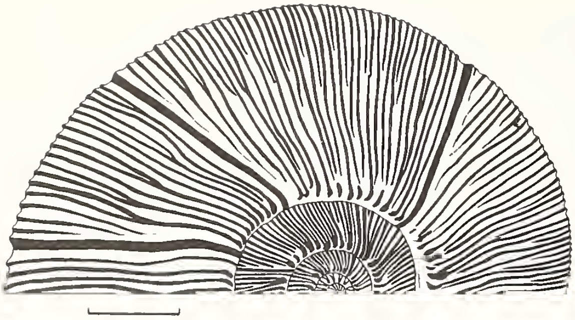


TEXT-FIG. 4. *Pavlovia* sp. Oxford University Museum, J35891; Hartwell, south-west of Aylesbury, Buckinghamshire; Portlandian. Shell section through a constriction (c) and subsequent rib (r). Nacreous lamellae wedge out at the adoral slope of the rib, whereas lamellae corresponding to the next secretion cycle can be seen emerging at the inner side of the rib (bottom left). Growth direction is to the left. Composite scanning micrograph; × 70.

thickened the definitive aperture, and when *Pavlovia* made a new constriction, the strategy became a very different one, that of resistance to shell breakage and peeling (see Kennedy and Cobban 1976). In this way, apertures could have played two defensive roles depending on the state of calcification.

Therefore, the major function of ribs strictly as reinforcement of the very apertural margin, invoked by Kennedy and Cobban (1976) and Checa and Westermann (1989), is at least debatable, as soon as submature stages are concerned. Rather, they must have prevented peeling of the shell some distance from the aperture backwards.

Constrictions do not usually coincide with the preceding costae and are more forwardly inclined (Checa and Westermann 1989), this being especially true for involute shells. The next ribs immediately after the constriction are always parallel to it. In general it seems as if the aperture deviated progressively from its ideal orientation (relative to shell radius) and was reorientated at the constrictions. This could be true in the strictest sense since longitudinal shortening due to folding of the periostracum must have been more intense towards the venter, as in this zone the periostracum is more repeatedly folded (except for simple ribs). In this way a progressive change in aperture orientation could have taken place, which was compensated at the constriction. This deviation grew with the interval between constrictions. Involute shells display the greatest differences between the internal (umbilical) and external (ventral) spiral lengths and, at the same time, they display the greatest ratio of secondary or intercalary to primary ribs, since corrugations tend to have a uniform distribution along the shell (Checa and Westermann, 1989). The involute ammonite *Maorites* displays spectacular examples of intersection between ribs and constrictions (Text-fig. 5; for other examples, see Macellari 1986), and it can be seen how ribs become



TEXT-FIG. 5. Ribs and constrictions are non-congruent in *Maorites seymourianus* (Kilian and Reboul). Drawing of specimen in Macellari (1986, fig. 30/1, 2). Scale bar is 20 mm.

progressively deviated only from the division point to the venter, while primary ribs retain the same orientation. In the widely-umbilicated, multi-constricted *Pavlovia*, ribs and constrictions are similarly directed. This implies that non-constricted shells with divided ribs had to avoid apertural deviation in some way. They could have achieved this by folding the primary rib in a long-wave and high-amplitude fashion, as in *Rasenia* (see below and Text-fig. 6C), which accounts for the well-known fact that primary ribs are usually much more developed that their corresponding secondary ribs in many groups of ammonites.

As an additional advantage, corrugation of the viscoelastic soft body and of the periostracum led to sinusoidal folds. This is the strongest shape in compression, since having permanent and more or less constant curvature, it is the least prone to develop local bending (Gordon 1978; Wilmot 1990). Ammonite rib profile and distribution was therefore highly fitted to the protective role it had to perform. Wrinkles probably did not achieve the status of functional structures. They were rather a fabricational noise (in the sense of Seilacher 1973) arising from the very process of construction.

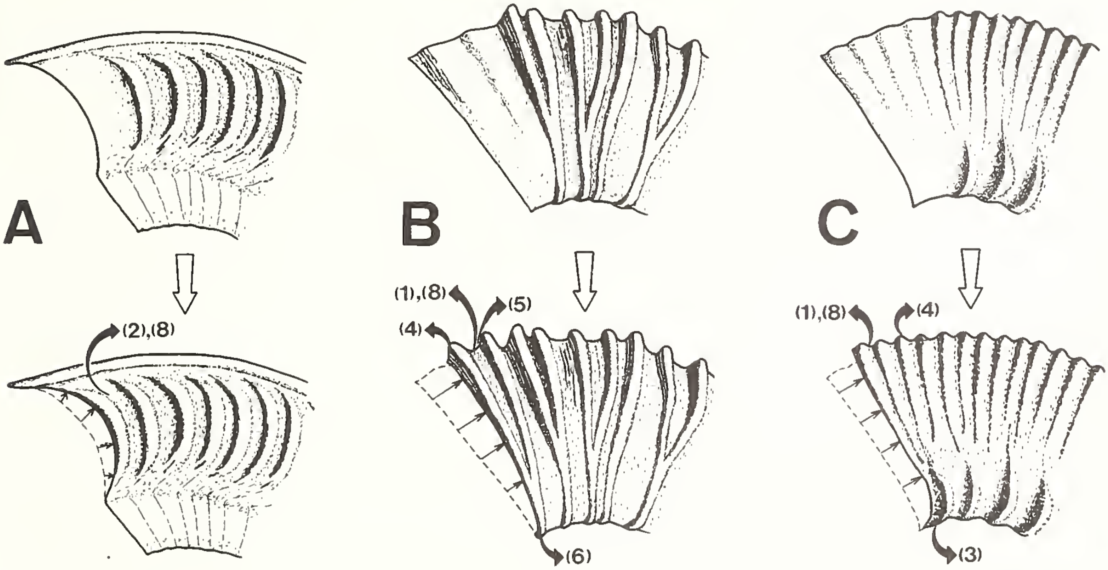
The exact advantages of the present concertina-like pattern of rib construction over other alternatives are not easy to determine, although it obeys a major rule: it is simple. It surely required less genetic instructions than the alternative of, for example, widening the apertural mantle periodically. This last strategy would have also obliged ammonoids to calcify each growth increment immediately after its secretion; otherwise, rib shape could not have been maintained.

A MORPHOGENETIC MODEL FOR AMMONITE RIBS

The process of folding of the periostracum

One of the main problems concerning the present model is the morphology and distribution of the muscular part responsible for the repeated folding of the periostracum, which must have been located orally. From the available data, there are two possibilities. Folding could have been brought about by the contraction of narrow longitudinal muscles attached to the inner surface of the periostracum (leading to longitudinal lines or bands on the shell). Traction along these lines could explain adorally concave wrinkles associated with longitudinal lines (8), but not costal bulges in themselves. Additionally, growth lines do not become significantly deviated when crossing longitudinal lines of attachment, which implies that they were not effective retraction lines.

A more likely hypothesis is that more or less inert lines of attachment of the periostracum to the mantle epithelium existed, while contraction was effected by an active oral muscular area. Palframan (1969) referred to oral muscle scars from *Hecticoceras*. When folding occurred, the periostracum was compressed radially at the intercostal valleys (Text-fig. 3), originating longitudinal and adorally convergent wrinkles, according to rib shape. At the same time the periostracum was dragged backwards, but, given its flexibility, it remained slightly behind the underlying soft body epithelium at the areas between attachment lines. This gave rise to longitudinal shear stresses between attachment lines and the areas between them. If dragging was not homogeneous along different attachment lines (as was probably the case with hildoceratins, Text-fig. 6A) shear stresses also arose between adjacent lines. Shear stresses originated by dragging of the periostracum led to the generalized formation of adorally convex wrinkles. Minor differential displacements between periostracum and the soft body also arose from the folding process, in such a way that the periostracum must have slid somewhat upslope on both rib sides (Text-fig. 3). Differential displacements created at the areas between attachment lines both by dragging and folding of the periostracum would have combined together at the apical slopes of ribs but would have counteracted each other at the adoral ones. This explains why longitudinal lines and their associated wrinkles initiate well down the adoral slope of the rib, but tend to invade the rib crest from the rear.



TEXT-FIG. 6. Proposed modes for the construction of ribs in different groups of ammonites, with indication of the kinds of microsculptures (numbers between parentheses) which are most likely to be formed in each case. Top row, prefolding stage; bottom row, postfolding stage, with prefolding outline insinuated (broken line). A, Hildoceratinae, folding was local and inhomogeneous and each folding event led to a single rib. B, *Pavlovia*, contraction affected the whole peristome inhomogeneously and a bifurcate rib was formed after a single folding event. C, *Rasenia*, *Pararasenia*, the whole uncalcified peristome contracted more or less homogeneously leading both to fasciculate secondary ribs and to a single wide primary rib. In B and C secondary ribs were already insinuated in the prefolding stage.

In summary, two different scale folds developed on the shells of ribbed ammonites. Long-wave folds (ribs) were created by muscular contraction of the soft body epithelium lining the shell, while short-wave transversal folds (wrinkles) developed exclusively on the periostracum.

Although this picture could have had a general applicability, differences in the folding process arose between different ammonites. In simple-ribbed hildoceratins it is clear that each retraction and contraction episode led to a rib (Text-fig. 6A). This was not obviously the case of ammonites with divided ribs. Traumas and abnormalities are always useful as natural experiments, and this study is not an exception. In one specimen of *Pararasenia* (Pl. 4, figs 1–2) the shell had been severely injured (peeled back) for, at least, some 30 degrees. Growth after the injury was characterized by anomalous ribs, in the sense that they were too low and too widely spaced. The most immediate explanation is that the animal was no longer able to fold the periostracum completely or in part, since the oral muscular area responsible for this process had been bitten away. The capability to make normal ribs was regenerated some one-quarter whorl after the injury, when primary ribs reappeared. Therefore, we are possibly contemplating the shape of the periostracum in its unfolded state. This case supports the hypothesis of an active muscular area in addition to attachment lines, since here muscular contraction presumably did not take place, but attachment lines were never lost after the injury. Retraction did not occur in this *Pararasenia* by teratological reasons, leading to a deflated periostracum, with lines of attachment to the soft body rising from the background. Otherwise, contraction of the soft body would have inflated the rib, and its surface would have bulged smoothly. Note also that in the specimen alluded to secondary ribs are only insinuated, while primary ribs are totally absent during the anomalous stage. This allows me to offer an explanation for the construction of divided (fasciculated) ribs in *Pararasenia*. The body advanced the whole length of the fasciculation to be created, while secreting a periostracum which was only slightly corrugated from the middle flank to the venter (Text-fig. 6c). Then forward motion ceased and the body contracted. Several short-wavelength, small amplitude folds were created at the upper flank according to the previous smooth corrugations, while a single, long-wavelength and high amplitude fold formed at the lower flank, originating the primary rib. Calcification presumably proceeded afterwards. This can possibly be applied to other (perhaps most) genera with divided ribs. In this way, a more or less homogeneous contraction along the whorl cross-section occurred, which may explain why primary ribs are usually much more developed than their corresponding secondary ribs (which is also a common figure in many groups of ammonites) and why apertural deviation did not take place in non-constricted shells with divided ribs (see above).

The case of *Pavlovia* (Text-fig. 6b) could be considered as intermediate, since presumably divided ribs were formed according to a *Pararasenia*-like pattern, with insinuated primary ribs. Nevertheless, contraction in *Pavlovia* was not so homogeneous as in *Pararasenia*, but, judging by rib profile, contraction increased from the umbilical seam to the venter.

Conclusion: the sequence of events

As evidenced by the above features, ribs, at least for Jurassic and Cretaceous ammonites, are compressional features, i.e. they are folds in the mechanical sense of the term. Their formation cycle could be as follows (Text-fig. 6).

(1) The soft body advanced beyond the last-formed aperture while continuously secreting a periostracum. This initial layer was not at all or only slightly folded.

(2) When this periostracum was extended to the length of a new rib, retraction of the soft body took place, which was attached to the periostracum at certain lines; folding of the periostracum then occurred, giving rise to a non-calcified rib. In constricted forms, this process was repeated until a new constriction was to be formed. Then the aperture rotated slightly forward and folded once again to form the constriction and subsequent rib.

(3) Calcification of the newly-formed rib or ribs began slightly prior to, or at, the same time as a new cycle was to be initiated with periostracal growth beyond the aperture. In constricted forms a new secretion cycle did not begin until the previous shell was fully calcified.

The segmental growth model revised

When Checa and Westermann (1989) proposed the segmental growth model, they based their argument on the intuitive notion that ribs were secreted as the juxtaposition of (immediately) calcified growth increments. Therefore, they assumed implicitly that the body mantle had to widen and contract repeatedly at the apertural edge. They found a perfect parallelism between growth lines and ribs in more than 150 ammonite genera. Therefore, the peristome had to change its orientation and shape to accommodate the variable morphology of divided ribs (see their fig. 1). As stated above, this is obviously not the case, but the geometric coincidence between ribs and growth lines makes sense also in the 'concertina' model if muscular attachment areas allowing retraction of the periostracum were distributed around the mouth. The new material also reveals that ribs are not always parallel to growth lines, since sometimes the folding axis of the new uncalcified ribs bisected growth lines at low angles. This has been observed in hildoceratins (Pl. 2, figs 2–3, 5; Pl. 3, figs 1–3), *Kosmoceras* (Pl. 5, fig. 3) and, more exceptionally, in *Pavlovia*.

THE ORIGIN OF THE FEATHER-LIKE ORNAMENT

This kind of ornament consists in a series of forwardly directed chevron-like wrinkles. It was figured and described in *Placenticeras* (Hyatt 1903, pl. 47), in Bathonian and Oxfordian oppeliids (Waagen 1869, pl. 18, fig. 5; Petitclerc 1918, fig. 1) and in *Taramelliceras* (Hölder 1955). Arkell *et al.* (1957) also referred to this ornament in examples of the Bajocian *Protoecotraustes* and the Albian *Beudanticeras* and *Brewericeras*. I have recognized feather-like microculptures in specimens of *Tragophylloceras* (Pl. 5, fig. 4), *Oxynoticeras* and several Hildocerataceae (Pl. 2, figs 4–5) (see also Table 1).

Seilacher (1988) considered these structures to be the insertion of retractor muscles. He probably based his view on the assertion of Arkell *et al.* (1957, p. L92) that in *Placenticeras* feather structures are 'apparently confined to the structure of the inner shell layers'. This is certainly not the case, since the only specimen of *Placenticeras* with the outermost shell preserved (*Pl. meeki*, C22686 in Table 1) displays well marked feather-like wrinkles. This applies also to the other genera listed in Table 1 displaying microsculpture (2). Therefore, this rare ornament was not internal (as assumed by the muscular hypothesis), but external. In *Placenticeras* external wrinkles are easily transmitted to the inner mould surface given the extremely thin shell borne by this genus (see thickness data in Westermann 1971, fig. 7). Individual wrinkles may sometimes span the whole space between the widely spaced, low-relief ribs, although the whole pattern may be interrupted at some definite growth lines (Pl. 6, fig. 3). Nor does this figure conform to a muscle attachment model.

Additionally, feather-like wrinkles do not display homology; they are exclusive of ammonites bearing concave ribs and can be reproduced easily in laboratory experiments (Text-fig. 2B). All these facts allow me to propose a compressive origin for feather-like ornaments, as a long-wavelength variant of adorally convergent wrinkles.

GROWTH LINES IN ARIETITIDAE AND EODEROCERATIDAE

In the specimens of Arietitidae and Eoderoceratidae listed in Table 2 I have recognized a very striking feature which is not mentioned in Table 1. In these specimens growth increments are very distinctive and, importantly, the wide growth lines bounding them are low- or high-relief depending on whether they are placed at one intercostal valley or at one rib height (Pl. 6, fig. 4). Sometimes (e.g. in *Caenisites brooki*) they are discontinuous in a stamp edge manner. This striking distribution could have constituted a different strategy to aid in folding the periostracum. Growth lines, which were lines of structural weakness, would have served the function of hinge lines between growth increments. Hinge (growth line) relief would have also determined the concavity of the folds, so that low-relief lines led to concave folds (intercostal valleys) and high-relief lines to convex folds (ribs). This system easily allows for radial folds to be created, but not for folds of other shapes (e.g. concave), being therefore well suited for the construction of wide radial ribs typical of arietitids and eoderoceratids. Note that two of the species listed in Table 2 also display compressive features (Table 1), although longitudinal lines (type 8) have been never found. If these ammonites lacked definite attachment lines of the periostracum to the soft body, this system of joints would have helped to fold the periostracum, thus avoiding inadequate defects. Nevertheless, observations are so fragmentary that no definitive conclusions can be reached here.

TABLE 2. List of specimens with 'arietitid-like' system of joints between growth increments (see text). All are housed at the Natural History Museum, London.

Taxon	Age	Locality	Registration No.
Arietitidae			
Arietitidae sp.	Lower Lias	Timsbury (near Radstock)	C41785
Agassiceras sp.	Sinemurian	Weston on Avon (Gloucestershire)	C16532
	Sinemurian	Pebworth (Gloucestershire)	C17455, –6
Euagassiceras resupinatum (Simpson)	Sinemurian	Pebworth (Gloucestershire)	C16269
Asteroceras confusum Spath	Sinemurian	Bredon (Worcestershire)	C2223
Caenisites brooki (Sowerby)	Sinemurian	Lyme Regis (Dorset)	C1926, C47352, C75386
	Sinemurian	Charmouth (Dorset)	C56997
Eoderoceratidae			
Xipheroceras sp.	U. Sinemurian		C3710
Microderoceras birchi (Sowerby)	Sinemurian	Lyme Regis (Dorset)	C135

TUBERCLES AND RIBS: TOWARDS A FABRICATIONAL TERMINOLOGY

Tubercles are usually the remains on the internal moulds of longer spines which were closed-off at their base. Together with ribs and keels, tubercles are one of the most common kinds of ornament in ammonoids. The only previous documented study on tubercle fabrication is, to my knowledge, that by Checa and Martín-Ramos (1989), in which the mode of growth of spines in two aspidoceratid genera (Upper Jurassic Ammonitina) is described (see their text-fig. 4). In *Aspidoceras* the long, delicate spines began as a horseshoe-shaped invagination at the shell aperture (i.e. parabolic node-like structure); the subsequent addition of incomplete, distorted rings of shell gradually formed a hollow, slightly conical spine which remained open at its tip. Spines could continue to grow even when the mantle moved forward beyond the tubercle limits. This pattern is similar to that reported for some Recent and extinct bivalves and gastropods. *Orthaspidoceras* has one periumbilical row of mammiform spines which grew at the same time as the mantle moved forward by the consecutive addition of protuberant waves of shell increments at the aperture. Therefore, there was no single mode by which ammonite spines were formed.

Even though ribs and tubercles may coexist on the same shell, it is clear that they are morphogenetically unrelated, that is, a fabricational continuum between both kinds of structures can hardly be envisaged. Therefore, the terms proposed for ammonoid ribbing by Arkell *et al.* (1957, pp. L90–L91) can be grouped into two classes on a fabricational base. Structures fabricated in a tubercle-like fashion would include spines, clavi and nodes (also parabolic nodes). Rib-related structures are plications, and bullae.

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Note added in proof. In two previously unreferred to papers Enay and Dominjon (1964, 1967) reported the presence of feather-like ornament in several species of the oppeliids *Trimarginites* (Oxfordian) and *Oxycerites* (Bathonian) and list a set of related references. They also mentioned Kessler (1923) as the author first propounding the muscular attachment hypothesis for the origin of feather-like ornament.

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AN EARLY CRETACEOUS ORTHOCERID CEPHALOPOD FROM NORTH-WESTERN CAUCASUS

by L. A. DOGUZHAEVA

ABSTRACT. An orthocerid cephalopod is reported for the first time from the Lower Cretaceous deposits of the Caucasus. Discovery of this mollusc, *Zhuravlevia insperata* gen. et sp. nov., in such young beds shows that evolution of the orthocerid branch within the cephalopods was not terminated in the Late Triassic, as was formerly believed, but continued for a further 90–95 Ma, at least until the late Aptian (Clansenian). *Z. insperata* was found in association with numerous and diverse Aptian ammonites, rare belemnites, and a single phragmocone-bearing coleoid *Naefia*, characterized by the absence of the guard, all comprising the cephalopod fauna of the shallow Aptian sea in the Hokodz River Basin. SEM studies of *Z. insperata* and *Naefia* recovered from the same Aptian concretions have shown that the former possesses lamellar nacreous ultrastructure of the septa common for cephalopods with an external shell, while the latter possesses granular nacreous ultrastructure of the septa common for cephalopods with an internal shell. The ultrastructure of the septal neck of *Z. insperata* is closely similar to that of previously studied Carboniferous orthocerids from the Buckhorn Asphalt, hitherto the only orthocerids studied with well preserved primary ultrastructure.

IN the process of splitting numerous Aptian concretions collected by the author in the Hokodz River Basin (Text-fig. 1), a small fragment of a 13 mm long subcylindrical orthocone, with four chambers preserved, was noticed on a freshly broken surface. It could easily have been mistaken for an aulacocerid or belemnite if it were not for the septa at both ends of the orthocone distinctly displaying the central position of the siphuncle (Pl. 1, figs 1–3). Closer examination revealed additional morphological features supporting its classification as an orthocerid: (1) the thickness of the shell wall and septa are greater than in belemnites from the same nodules; (2) the outer surface of the shell exhibits fine growth lines common in orthocerids but uncommon in belemnites; (3) the septa are oblique, being attached to the shell wall closer to the aperture on one side (assumed dorsal) than on the other (assumed ventral) side, as known in other orthocerids (Zhuravleva 1978, pl. 6, fig. 7).

Ultrastructural studies of the orthocone demonstrated that the shell wall, septa, and septal necks are similar to those of Carboniferous orthocerids (Erben *et al.* 1969; Ristedt 1971; Mutvei 1972; Blind 1988). However, while the ultrastructure of the shell wall and septa in orthocerids is the same as in other ectocochleate cephalopods, that of the septal neck is of the type found only in orthocerids (Pl. 2).

Thus there is no doubt that this orthocone from the Aptian Stage is an orthocerid cephalopod. This find is surprising as orthocerids have not previously been found in beds younger than Late Triassic. The orthocerids first appeared in the Ordovician and the acme of their development was in the Devonian. After that time they gradually declined until only three genera remained in the Triassic (Jeletzky and Zapfe 1967; Schastlivceva 1988; Bizzarini and Gnoli 1991). However, during that period they had an extensive geographical distribution. For example, about forty species of the single genus *Trematoceras* are known from Upper Triassic beds in the Eastern Alps, the Himalayas, Timor, New Zealand, and North America. In the former USSR, orthocerids have been reported from Lower and Middle Triassic deposits of the Maritime Territory, Eastern Siberia, Mangyshlak, Verkhoyanye, and North Caucasus (Schastlivceva 1988). In this last region, two species of *Paratrematoceras* were found in Middle Triassic deposits from a section in the Tkhach River Basin (Schastlivceva 1988). No orthocerids have yet been reported from Jurassic strata.

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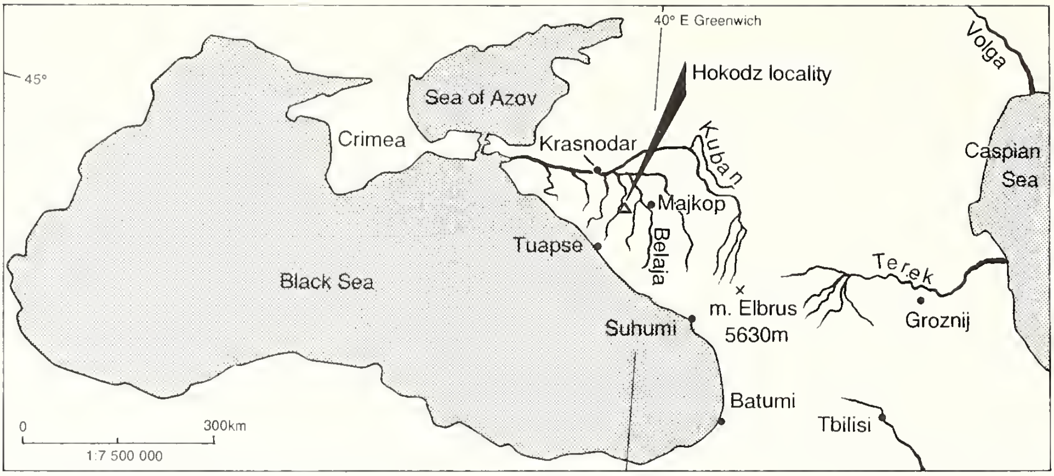
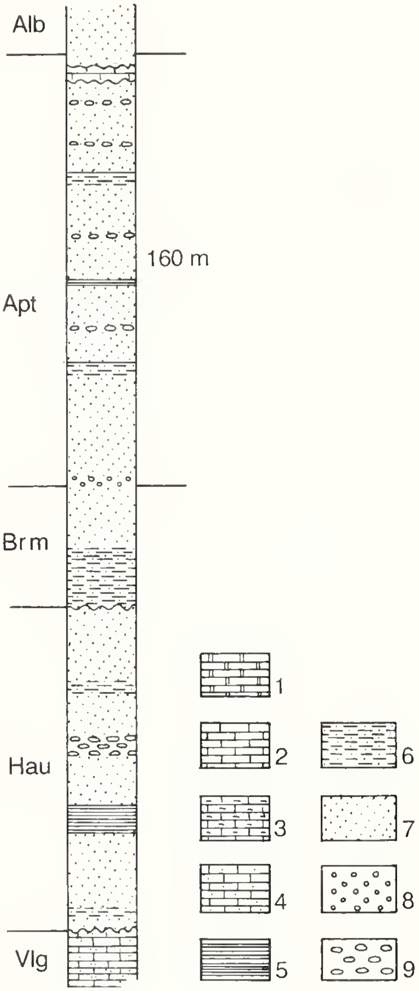


TEXT-FIG. 1. Generalized locality map showing the approximate position of the Hokodz locality.



TEXT-FIG. 2. Stratigraphical position of the horizon with *Zhuravlevia insperata* gen. et sp. nov. Adapted from Druschitc and Mikhailova (1966), with an upwards revision of the Aptian-Albian boundary. 1, dolomitic limestone; 2, limestone; 3, argillaceous limestone; 4, arenitic limestone; 5, clay; 6, siltstone; 7, sandstone; 8, conglomerate; 9, concretions.

The presence of an orthocerid in the Lower Cretaceous is unexpected. Its occurrence in such young deposits could not have been the result of reworking from older strata as there is no evidence of stratal disturbance. In the Mesozoic of the northwestern Caucasus, there is a layer-cake stratigraphy (Mitin 1965). Middle Triassic beds (which have yielded orthocerids) are overlain by the Upper Triassic, on which rest Jurassic strata. The latter are overlain by the Lower Cretaceous, all six stages of which are recognized. Further evidence that the orthocone under discussion has not been reworked is the nature of preservation of the shell material, which is the same in both the orthocone and the associated ammonites: partly phosphatized shells of a brown colour with weakly recrystallized ultrastructure. Thus, the conclusion is that this orthocerid actually inhabited the Aptian sea of the north-western Caucasus. Why then, have orthocerids never been reported from this area which has been so thoroughly studied for over a hundred years? Three reasons can be considered: (1) they were not as common in life as the ammonites or belemnites; (2) their shells are slender orthocones of small diameter, even at adult stages; (3) they have small, straight shells which are rarely preserved in their entirety. The large hiatus in the orthocerid record in the north-western Caucasus, corresponding to the interval between the Anisian and Aptian stages, could be explained by the rarity or absence of favourable conditions for burial and fossilization of marine fauna.

GEOLOGICAL SETTING

In the north-western Caucasus, the Lower Cretaceous is widespread, extending in a narrow belt in an east-west direction. It is composed mainly of sandstones, clays, and siltstones, with marls and limestones at the base (Luppov 1952; Egoian 1965; Druschitc and Mikhailova 1966). In this region, the deposits encompass six stages, with a total thickness of about 600 m (Mitin 1965; Egoian 1965). The Aptian comprises clays, sandstones, and siltstones with a high concentration of glauconite and numerous sideritic concretions. Its total thickness is about 160 m (Text-fig. 2), and ammonoids are common which makes it possible to trace the zones here (Text-fig. 3). The

Albian	Lower substage	Zone of *Douvilleiceras mammilatum* Zone of *Leymeriella tardefurcata*
Aptian	Clansenian Substage	Zone of *Diadochoceras nodosocostatum* and *Acanthohoplites bigoureti*
	Gargasian Substage	Zone of *Parahoplites melchioris* and *Colombiceras tobleri* Zone of *Epicheloniceras tschernyschewi* and *Colombiceras crassicostatum*
	Bedulian Substage	Zone of *Deshayesites deshayesi* Zone of *Deshayesites weissi* and *Procheloniceras albrechtiaustriae*
Barremian	Upper substage	'Zone' of *Heteroceras astierianum*

TEXT-FIG. 3. Ammonoid zones of the Aptian of north-western Caucasus (after Egoian 1969).

sandstone–siltstone sediments are poorly graded and the abundance of quartz gravel and carbonized wood indicates the existence of a shallow-water continental sea during this time (Mitin 1965). As evidenced through spore and pollen analysis, the profusion of Gleicheniaceae (40 per cent) and Pinaceae (34 per cent) is an indication that deposition occurred during a temperate climate regime (Rimsha and Serdjukova 1965).

The uppermost Aptian (Clansenian) of the Hokodz River Basin, from which the orthocone under discussion was collected, contains numerous sideritic concretions with well-preserved gastropods, bivalves, and carbonized wood and pine cones, together with an extremely rich ammonite assemblage. The most common ammonite genera, comprising about 100 species, are: *Euphylloceras*, *Phyllopachyceras*, *Tetragonites*, *Ptychoceras*, *Melchiorites*, *Diadochoceras*, *Acanthohoplites*, and *Hypacanthoplites* (Pl. 1, fig. 6). Some species found in this section occur frequently in the Clansenian stratotype in southwestern France. However, many others are endemic (Egoian 1965, 1969). Only two belemnite genera, *Mesohibolites* and *Neohibolites*, are known from this section, and are rare. Recently, three incomplete coleoid phragmocones identified as *Naefia* (Pl. 1, figs 4–5) have been found here by the author (paper in preparation).

SYSTEMATIC PALAEONTOLOGY

Order ORTHOCERIDA Kuhn, 1940
Superfamily ORTHOCERATACEAE M'Coy, 1844
Family GEISONOCERATIDAE Zhuravleva, 1959
Genus ZHURAVLEVIA gen. nov.

Derivation of name. Named in honour of F. A. Zhuravleva, in recognition of her major contribution to our knowledge of ancient cephalopods.

Type species. *Zhuravlevia insperata* sp. nov.

Type locality. Hokodz River Basin, north-western Caucasus.

Horizon. Lower Cretaceous, Upper Aptian (Clansenian).

Diagnosis. Small, slender orthoconic shell, circular in cross-section, gradually increasing in diameter towards the aperture. Sutures slightly oblique. Siphuncle central and narrow; necks short and suborthochoanitic; connecting rings thin and expanding slightly within the camerae. Camerae long. Surface with fine growth lines.

Comparisons. Differs from Ordovician to Devonian *Geisonoceras* Hyatt, 1884 and Lower Triassic *Pseudotemperoceras* Schastlivceva, 1986 in having a central siphuncle and longer camerae (1·50–1·70 of shell diameter compared with 0·40–0·45 for *Geisonoceras* and 0·25–0·30 for *Pseudotemperoceras*).

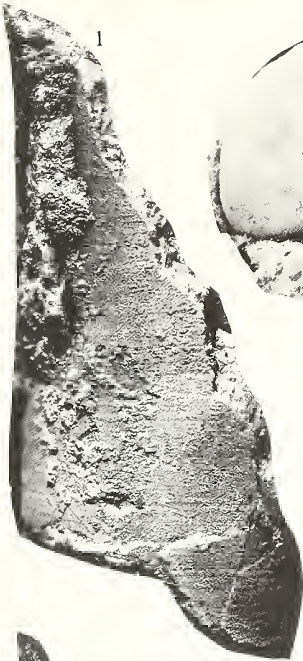
EXPLANATION OF PLATE 1

Figs 1–3. *Zhuravlevia insperata* gen. et sp. nov.; 3871/123 PIN. 1, outer surface of orthocone with visible growth lines; × 6. 2, fifth septum from body chamber with central opening for siphuncle; × 7·5. 3, medial section of orthoconch showing central position of siphuncle; × 7·5.

Figs 4–5. *Naefia* sp.; 3871/124 PIN. 4, lateral view with marginal siphuncle on left; × 6. 5, medial section showing position of siphuncle and structure of septal necks; × 8.

Fig. 6. Piece of concretion with ammonite shells; a, *Diadochoceras*; b, *Ptychoceras*; c, *Melchiorites*; d, *Euphylloceras*; × 1. All specimens from the Clansenian, Aptian; Hokodz River basin, NW Caucasus, Russia.

PLATE 1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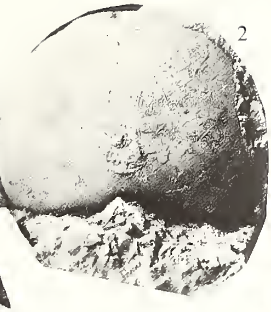
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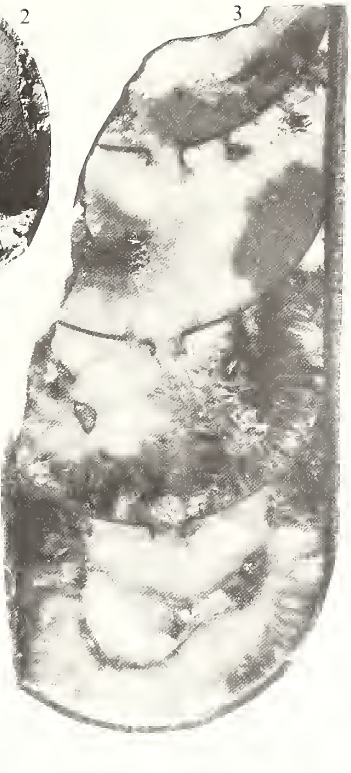
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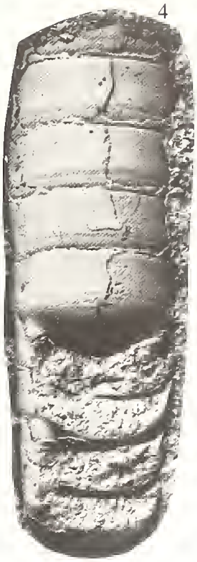
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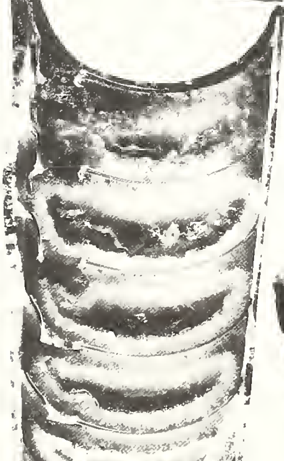
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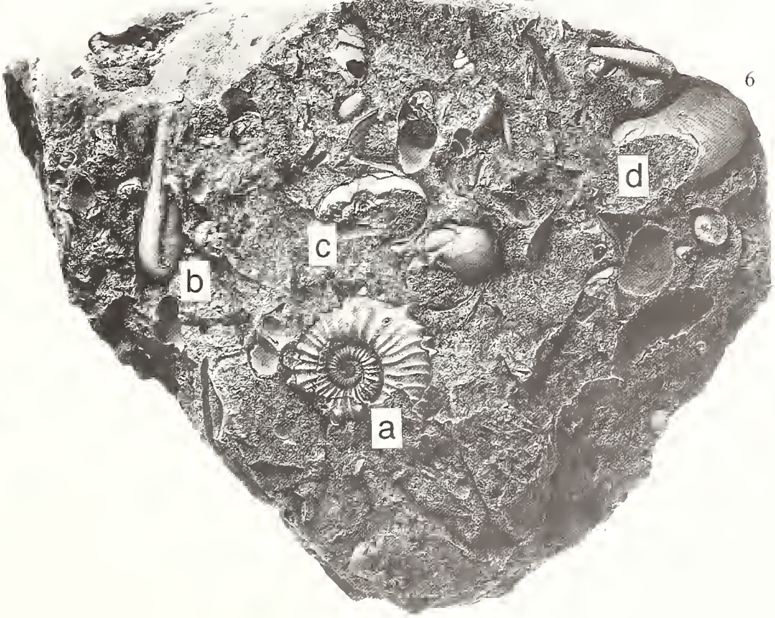
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DOGUZHAEVA, *Zhuravlevia*

Remarks. The new genus is based on a single specimen representing the part of the phragmocone that adjoins the body chamber. Siphonal and cameral deposits were not formed in the fragment recovered. Therefore the new genus is assigned provisionally to the family Geisonoceratidae, primarily on the basis of the configuration of the septal necks, position of siphuncle, and resemblance to the genus *Pseudotemperoceras. Zhuravlevia* is similar to the latter in shell morphology and in the absence of siphonal and cameral deposits in the camerae adjoining its body chamber. However, Schastlivceva (1988) considered the inclusion of *Pseudotemperoceras* within the geisonoceratids as tentative, because of the significant stratigraphical gap between the occurrence of it and other geisonoceratids previously discovered (middle Ordovician-Lower Triassic). For the same reason, the assignment of *Zhuravlevia* to the geisonoceratids is also tentative.

Zhuralevia insperata sp. nov.

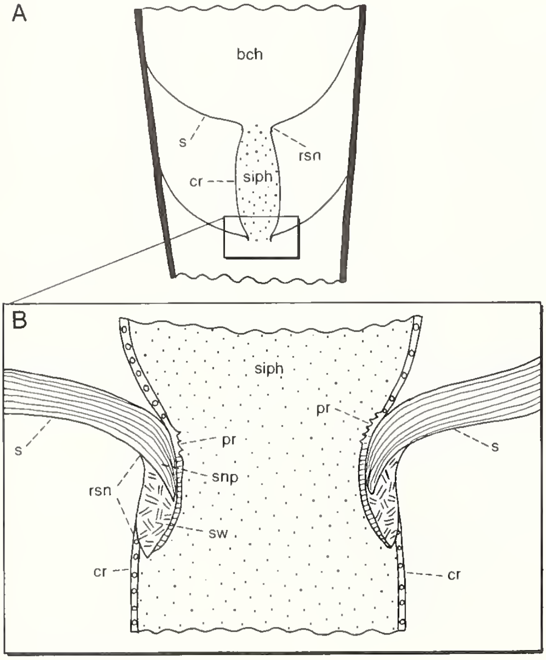
Plate 1, figures 1–3; Text-figure 4

Derivation of name. From Latin *insperata* – unexpected, alluding to its unusually high stratigraphical position.

Holotype. 3871/123, Palaeontological Institute, Russian Academy of Science, Moscow.

Type locality. Hokodz River Basin, northwestern Caucasus.

Diagnosis. Small, slender orthoconic shell, circular in cross-section. Available fragment of the phragmocone is 13 mm in length and 6 mm in maximum diameter. Angle of expansion 5 to 6°. Surface with fine, indistinct transverse growth lines. Length of camerae 1·5 to 1·7 their diameter. Suture oblique. Siphuncle central and narrow, length about 1·7 the diameter of the phragmocone. Connecting rings thin, slightly expanding within the camerae (Text-fig. 4A–B). Length to width ratio of segments is about 3·5. Diameter of the septal foramen is 0·5 the diameter of the segment. Necks suborthochoanitic, very short, about 1·13 the length of the camerae. Siphonal and cameral deposits unknown.



TEXT-FIG. 4. Schematic medial sections of a chamber in *Zhuravlevia insperata* gen. et sp. nov. A, position and shape of siphonal segment. B, structure of septal neck, consisting of septal neck proper and additional swollen part, with thin connecting ring adjoined to the latter. Legend: bch, body chamber; cr, connecting ring; pr, prismatic layer; rsn, retrochoanotic septal neck; s, septum; siph, siphuncle; snp, septal neck proper; sw, swollen additional part of the septal neck.

ULTRASTRUCTURE OF THE SHELL

Shell ultrastructure in *Z. insperata* has been studied to obtain additional criteria elucidating the classification of this form within the cephalopods. Based upon morphological characters alone, placement of this orthoconic cephalopod within the orthocerids or in some unknown coleoid group with a central siphuncle is uncertain. Therefore details concerning the ultrastructure of the specimen have been compared with available data on the orthocerids and for undetermined fossil coleoids from the same concretions.

Modern knowledge of the ultrastructure of the orthocerid shell is based upon studies of material from the Pennsylvanian (Upper Carboniferous) Buckhorn Asphalt of the USA (Erben *et al.* 1969; Ristedt 1971; Mutvei 1972; Blind 1988). The Buckhorn Asphalt provides the only locality where orthocerids with a well-preserved primary shell ultrastructure have been collected. The shell wall in these orthocerids is composed of the outer prismatic, nacreous, and inner prismatic layers. The septa consist primarily of a nacreous layer with a spherulitic-prismatic layer along the periphery. A prismatic layer forms a prominent ridge around the entrance to the septal neck. Nacreous ultrastructure on the concave adoral face of the septum is modified by the presence of fairly thick conchiolin membranes, whereas in the largest remaining portion of the septum these membranes are thin and regularly spaced. The septal necks consist solely of a continuation of the nacreous layer forming the septa. The inner surface of the most proximal portion of the neck is covered by a thin prismatic layer. The distally swollen region of the neck is distinctly separated from the proximal part, which has a strongly modified ultrastructure. According to Mutvei (1972), the conchiolin membranes of the septal necks continue to the structurally modified part, but the nacreous lamellae are replaced by prismatic lamellae. Blind (1988) described the swollen portion of the septal neck as spherulitic and assumed that the siphuncular epithelium bordered by spherulitic prisms was anchored to the septal neck after deposition of the outer connecting ring. The connecting ring consists of two layers: the outer of uncalcified conchiolin and the inner prismatic (Mutvei 1972). The conchiolin layer of the connecting ring occasionally contains dispersed spherulites (Blind 1988).

In the four chambers immediately preceding the body chamber, the siphuncle was covered only by the outer conchiolin layer, and the inner prismatic layer appeared at the fifth chamber (Blind 1988). Therefore, secretion was retarded.

Preservation of the Caucasian Aptian orthoconic shell is sufficient to allow study with the SEM. However, the level of detail observed in the material examined from the Buckhorn Asphalt was not obtained in the Aptian material. As in the orthocerids from the Buckhorn, the shell wall consists of three layers. The nacreous layer is the thickest portion of the wall, while the prismatic layers are comparatively thin. Septa are one-third the thickness of the shell wall, and consist primarily of the nacreous layer (Pl. 2, fig. 3). The narrow adapical portion of the septum differs from the remaining part in the presence of fairly thick conchiolin membranes. The nacreous layer possesses a columnar type structure common for the septa of the ectocochleate cephalopods.

The septal necks are separated into two regions by a distinct boundary (Pl. 2, figs 2–4; Text-fig. 4B). The septum passes into the septal neck proper which, consequently, is nacreous. The septal neck proper then decreases in thickness in the adapical direction. The adapical region adjoining the septal neck proper from outside is larger and usually swollen (Pl. 2, figs 2–4; Text-fig. 4B). Unlike the septal neck proper, the swollen part does not pass into the septum. The inner surface of the septal neck appears to be invested by a thin prismatic layer (Text-fig. 4B).

Connecting rings are not preserved except for the small parts adjoining the septal necks, but they are indicated by the shape of the segments of the siphuncle within the chambers (Pl. 2, figs 2, 4; Text-fig. 4B).

From this discussion, it is clear that the shell ultrastructure of *Z. insperata* is similar to that of the Pennsylvanian orthocerids. The unique structure described here in the septal necks is known only in the orthocerids. Ultrastructural studies of the coleoid *Naefia* from the same Aptian concretions (Pl. 2, fig. 5) show that the septa are composed of granular crystallites (Pl. 2, fig. 5). Intralamellar organic membranes which subdivide the septal nacre into thin mineral lamellae in the ectocochleate cephalopods are absent here, while the nacreous layer of the shell wall is not modified and shows lamellar ultrastructure. The same difference between the septal nacre and shell wall nacre is well known in other coleoids (Mutvei 1970, 1984; Dauphin and Kelle 1982; Hewitt *et al.* 1991). In contrast, in *Z. insperata* the nacre of the septa and of the shell wall is of the same type, resembling in this respect other ectocochleate cephalopods. Thus, the septal ultrastructure in *Z. insperata* convincingly supports its belonging to the ectocochleate cephalopods and the ultrastructure of the septal necks confirms its placement in the orthocerids.

PHYLOGENETIC IMPLICATION

The Aptian orthocerid described above as *Zhuravlevia insperata* shows that the evolution of the order Orthocerida was not terminated in the Late Triassic as previously believed, but continued at least 90–95 Ma longer, to almost the middle of the Cretaceous.

Teichert (1988) combined the Orthocerida with the Plectronocerida (Upper Cambrian), Yanhecerida (Upper Cambrian), (?) Protactinocerida (Upper Cambrian), Ellesmerocerida (Upper Cambrian-Ordovician), Ascocerida (Middle Ordovician-Upper Silurian) into the subclass Orthoceratoidea Kuhn 1940. Teichert considered that this subclass was the central cephalopod stock, giving rise to all other cephalopods. The Orthocerida had a range of about 360 Ma, which is the longest among cephalopods.

The Aptian orthocerid shows that, together with Nautiloidea and Ammonoidea, the Orthoceratoidea crossed the Triassic–Jurassic boundary, although all of these groups were close to extinction. For the evolutionary pattern of the subclass Orthoceratoidea in post-Triassic time, one can use the term 'outage', introduced by Teichert (1988). Teichert used this to describe the crises which 'may occur during a prolonged interval during which the group virtually or completely disappears from the paleontological record…the group became so restricted in taxonomic scope and in habitat that fossil representatives are great rarities or have not yet been identified at all' (Teichert 1988, p. 70).

The shell morphology in *Z. insperata* exemplifies the strong morphological conservatism showed by the orthocerids during their evolution. The comparison of the septal neck ultrastructure in *Z. insperata* with that in Carboniferous orthocerids gives further indication of high morphological (ultrastructural) stability as a characteristic of the orthocerids. Unfortunately, absence of ultrastructural data for other orthocerids does not allow wider comparison. My attempts to study shell ultrastructure in Triassic orthocerids and pseudoorthocerids (described by Schastlivceva 1988) have not yet yielded results because of poor preservation of shell material. Preservation of the shell matter unfit for SEM studies can also be the reason for the lack of the ultrastructural information on orthocerids of other ages.

The fact that *Z. insperata* possesses a simple shell morphology gives additional confirmation to the idea that times of crisis for the cephalopods, such as at the Triassic–Jurassic boundary, were passed through by comparatively simply organized forms. However, the morphological features

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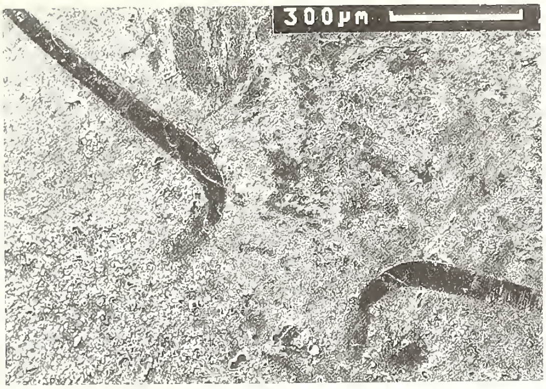
EXPLANATION OF PLATE 2

Figs 1–4. *Zhuravlevia insperata* gen. et sp. nov.; 3871/123 PIN; scanning electron micrographs of etched medial section of orthoconch. 1, general view of retrochoanitic septal neck; × 55. 2, enlarged left portion of septal neck shown in fig. 1, showing that it consists of the septal neck proper and an additional swollen part; × 325. 3, nacreous lamellar ultrastructure and columnar type of septum near septal neck; × 265. 4, right portion of septal neck, consisted also of the septal neck proper and an additional swollen part; thin connecting ring adjoining septal neck is distinctly visible in lower left corner; × 325.

Fig. 5. *Naefia* sp.; 3871/124 PIN; scanning electron micrograph of etched medial section of septum and retrochoanitic septal neck, showing differences in septum ultrastructure and septal neck structure compared with *Z. insperata*; × 240.

Both specimens from the Clansenian, Aptian; Hokodz River Basin, NW Caucasus, Russia.

PLATE 2



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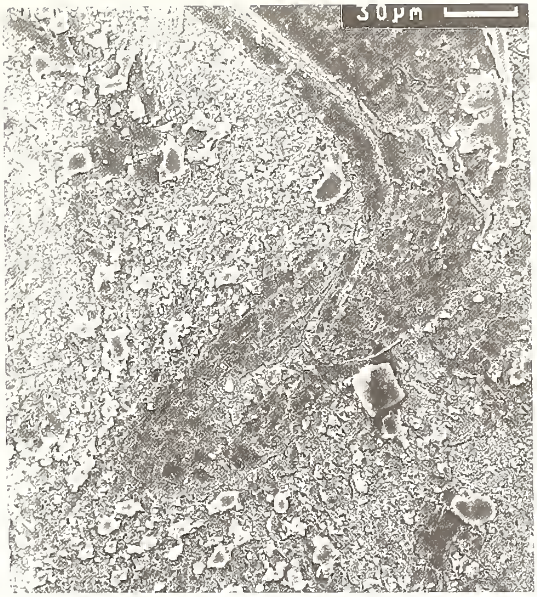

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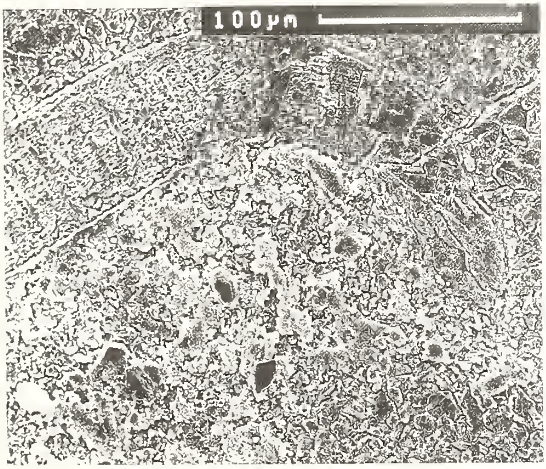

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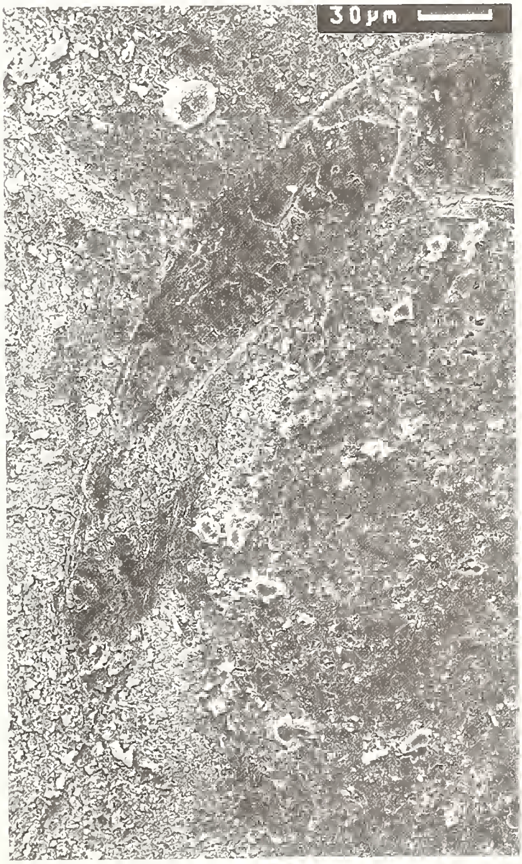

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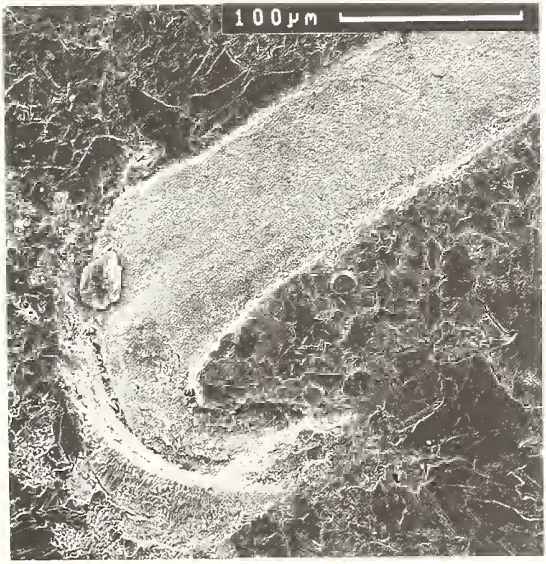

DOGUZHAEVA, *Zhuravlevia*

that made for survival are not yet adequately known. In this connection, the small size of the shell at adult ontogenetic stages in *Z. insperata*, indicated by the short last chamber of the phragmocone before the body chamber, is worth noticing. It is obvious that, if the Aptian orthocerids had medium-to-large-sized shells, they would have been found earlier, because the cephalopod assemblage in the Hokodz river locality is rich in taxonomic variety and number. So, the small size of the shells must have been a characteristic feature of these orthocerids.

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A NEW BARNACLE FROM THE LOWER JURASSIC OF SOUTH WALES

by P. HODGES

ABSTRACT. A previously unknown cirriped from the *semicostatum* Biozone of the Lower Lias of Bridgend, South Wales is described. The fused scutum and tergum, and the lack of any indication of a peduncle, indicates some loose affinities with the Verrucomorpha. However, the tooth-like nature of scutum and tergum are unlike the plate in any other known cirriped. A new taxon *Bassettina cambriensis* is assigned to a new family, the Bassettinidae.

DURING the excavation in 1982 of foundations for a new factory for the Ford Motor Company, in Bridgend, South Glamorgan, beds of Lower Jurassic limestones, mudstones and clays were exposed containing a rich fauna of silicified invertebrates. These beds were deposited in a shallow marine environment near several Early Jurassic 'islands' (Trueman 1922).

Ammonites identified from these beds indicate the *resupinatum* Sub-biozone. A large collection of silicified invertebrates was made including bivalves, gastropods, brachiopods, ammonites, belemnites and a few arthropods. Amongst the specimens collected were a number of problematica. The material described herein, housed in the Department of Geology at the National Museum of Wales (NMW), was collected from a yellow clay band (Hodges 1986) and has, until recently, remained unidentified. However, following a suggestion by Dr J. C. W. Cope, they are identified as barnacles.

SYSTEMATIC PALAEONTOLOGY

Superorder THORACICA Darwin, 1854
Order SESSILIA Lamarck, 1818
Suborder VERRUCOMORPHA? Pilsbury, 1916
Family BASSETTINIDAE fam. nov.

Diagnosis. Thoracica with hollow tooth-like plates, paired scutum, tergum and latus carinal plates fused together at base, scalloped basal margin, pit-like depression towards apex of tergum and scutum indicating possible site of muscle attachment, peduncle very short or absent.

Genera included. *Bassettina* gen. nov.

Discussion. The systematics of Thoracica currently recorded from the Mesozoic is as follows (Schram 1986; Newman 1987).

- Superorder THORACICA Darwin, 1854
  - Order PEDUNCULATA Lamarck, 1818
    - Suborder IBLOMORPHA Leach, 1825
      - Family IBLIDAE Leach, 1825
    - Suborder SCALPELLOMORPHA Pilsbury, 1916
      - Family SCALPELLIDAE Pilsbury, 1916
      - Family STRAMENTIDAE Withers, 1920

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Order SESSILIA Lamarck, 1818
  Suborder BRACHYLEPADOMORPHA Withers, 1923
    Family BRACHYLEPADIDAE Woodward, 1991
  Suborder VERRUCOMORPHA Pilsbury, 1916
    Family PROVERRUCIDAE Newman and Hessler, 1989
    Family VERRUCIDAE Darwin, 1854
  Suborder BALANOMORPHA Pilsbury, 1916
   Superfamily CHTHAMALOIDEA Darwin, 1854
    Family CATOPHRAGMIDAE Utinomi, 1968

The Iblomorpha includes cirripeds with a capitulum supporting two pairs of weakly calcified plates, and with scuta and terga having apical umbones. The peduncle is not separated from the capitulum, and is clothed with blunt chitinous spines. The Scalpellomorpha includes all cirripeds with a plated capitulum and plated peduncle. The Verrucomorpha consists of barnacles with an asymmetrical arrangement of plates, fixed and moving scuta and terga, and which lack a peduncle. The Brachylepadomorpha have a bilaterally symmetrical shell comprising rostrum and carina with a fixed base of imbricating scales, an operculum of paired scuta and terga, and which lacks a peduncle. The Balanomorpha have a bilaterally symmetrical shell comprising carina, rostrum and up to three pairs of plates variously fused, paired opercular valves, and which lacks a peduncle.

The phylogeny of the Thoracica has been discussed in detail in Newman *et al.* (1969) and partly revised by Newman (1987). The evolution of the sessicle barnacles has also been discussed in Newman and Hessler (1989). The scarcity of sessile barnacles in the Jurassic fossil record causes some difficulty in the interpretation of phylogenetic relationships between the three suborders. The point in the fossil record at which the sessile barnacles evolved from the pedunculate barnacles is also unresolved.

Only the Iblomorpha, Scalpellomorpha and Brachylepadomorpha are recorded in the Jurassic, with the Verrucomorpha and Balanomorpha first appearing in the Cretaceous. In the Lower Jurassic, the Iblomorpha are represented by *Eolepas* (Whyte *in* Briggs *et al.* 1993) and the Scalpellomorpha by *Archaeolepas* (Zittel 1885); the former is also recorded from the Triassic. Buckeridge and Grant-Mackie (1985) have also recorded a scalpellid barnacle from the Lower Jurassic of New Caledonia which they assigned to ?*Neolepas* (Newman 1979) a genus previously known only from the Holocene. The Brachylepadomorpha is represented in the Upper Jurassic only, by *Pycnolepas* (Withers 1914).

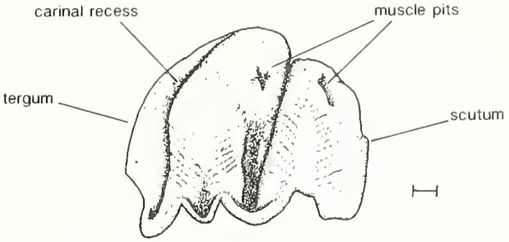
The diagnostic characteristics of *Bassettina* are the fixed scutum and tergum and the absence of a peduncle, and these indicate close affinities with the Verrucomorpha, as represented by *Eoverruca* (Withers 1935) and *Proverruca* (Withers 1914) from the Upper Cretaceous. However, the hollow tooth-like scutum and tergum are clearly very different from the plate-shaped scutum and tergum of genera of the Verrucidae. For this reason a new family, the Bassettinidae, is proposed to include genera with hollow tooth-like plates,

Genus BASSETTINA gen. nov.

Derivation of name. After Dr M. G. Bassett as a gesture for the help and encouragement given to me over many years.

Type species. Bassettina cambriensis gen. et sp. nov.

Diagnosis. Plates tooth-like, hollow, comprising paired scutum, tergum, latus carinal plates fused at base and a carina plate, peduncle very short or absent.



TEXT-FIG. 1. *Bassettina cambriensis* gen. et sp. nov. Descriptive features of inner surface of holotype, NMW 83.22G.856; drawing based on Text-figure 2E; scale bar = 1 mm.

Bassettina cambriensis sp. nov.

Text-figures 1–2

Derivation of name. From *Cambria*, the Latin name for Wales.

Holotype. NMW.83.22G.856 from the *resupinatum* Sub-biozone, *semicostatum* Biozone, Ford Motor Company Site, Bridgend, South Glamorgan, South Wales (locality SS 936782).

Paratype. NMW.83.22G.857 horizon and locality as for holotype.

Diagnosis. As for genus.

Measurements. (mm.)
Holotype, NMW.83.22G.856.

	Height	Length	Width
Tergum	11·3	8·0	5·5
Scutum	9·0	5·0	3·0

Paratype, NMW.83.22G.857.

	Height	Length	Width
Tergum	12·0 (est.)	8·0	6·0

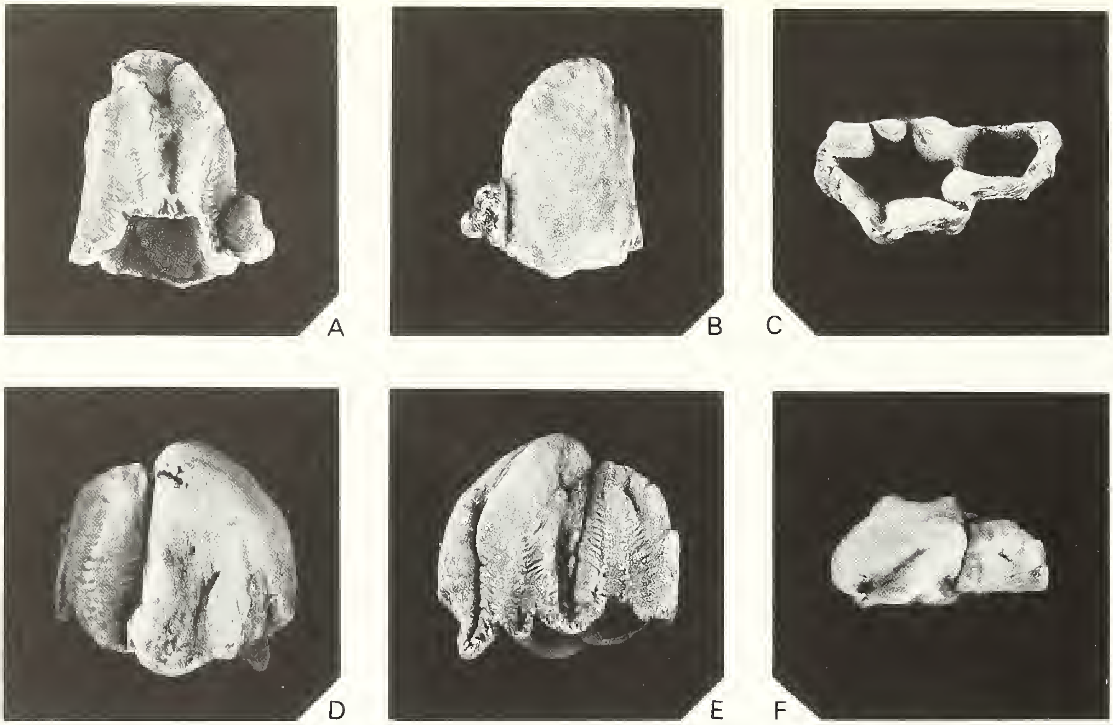
Description. The scutum and tergum are hollow, tooth-like and porcelaneous in appearance. They are fused at the base and have a scalloped basal margin. The tergum is blade-like in profile and the outer wall is rounded and relatively smooth. The carinal and scutal sides of the tergum are flattened at the interface with adjacent plates and ornamented with slightly sinuous parallel growth halts sloping at a few degrees downwards and towards the centre of the flattened carinal interface. The central portion of the carinal interface surface is elongated and triangular, and is smooth and devoid of growth halts where contact has been made with the adjacent plate. The remaining part of the tergum inner surface is either smooth or marked by irregular growth halts and is slightly concavely elongated towards the base. The carinal side of the tergum is marked by a deep groove running from apex to base which probably served as a recess for the carina. Towards the apex of the tergum on the inner side, is a pit-like depression, possibly the site of a muscle attachment. The opposite paired tergum is a mirror image in profile. There is evidence of a small fused tooth-like latus carinal plate at the base of the tergum on the carinal side.

The scutum is also blade-like in profile, smaller, and a mirror image of the tergum. The outer wall is rounded and generally smooth but growth halts are visible in parts. The interface with adjacent plates is ornamented as in the tergum. A short narrow pit is present just below the apex running parallel to the margin. This probably served as a position of muscle attachment. Carinal plate not seen, only evidence of its presence as exhibited by the carinal recess in the tergum.

DISCUSSION

The diagnostic characteristics of *Bassettina* are unlike those of any other genus in the Thoracica but, until further material has been collected from the Jurassic to clarify the early phylogeny of the sessile barnacles, it has provisionally been placed in the Verrucomorpha.

The scalloped base of the tergum and scutum does not lend itself to fixation to a flat surface, indicating the possible presence of a very short peduncle. This feature places the Bassettinidae



TEXT-FIG. 2. *Bassettina cambriensis* gen. et sp. nov. A–B, paratype, NMW 83.22G.857; A, inner surface of tergum; B, outer surface view of tergum. C–F, holotype, 83.22G.856; C, scutum and tergum viewed from below; D, outer surface view; E, inner surface view; F, scutum and tergum viewed from above. All specimens coated with ammonium chloride and magnified × 3.

somewhere intermediate in characteristics between the Brachylepadidae and the Verrucidae and the possibility exists that they all share a common ancestor. The absence of any other genera with hollow tooth-like plates at higher stratigraphical levels, indicates that the Bassettinidae may be an extinct family and, as such, was an evolutionary 'dead end'.

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IMMUNO-TAXONOMY AND THE RECONSTRUCTION OF BRACHIOPOD PHYLOGENY

by BERNARD L. COHEN

ABSTRACT. The proposed use of immuno-taxonomy of brachiopod shells for the reconstruction of brachiopod phylogeny is analysed for its possible contribution to genealogical systematics and for the validity of its principal conceptual and methodological foundations. It is concluded that brachiopod immuno-taxonomy, as so far described, departs from important norms of immuno-taxonomic and scientific procedures and can be of only limited utility in systematics.

IN response to an earlier critique (Cohen 1992), immuno-taxonomy has been defended as providing a timely and practical approach to brachiopod systematics (Curry *et al.* 1993). Although the concept of applying this methodology to the brachiopod shell is novel and worthwhile, and it has potential importance for palaeobiology, the alternative analysis given here suggests that its practical utility remains highly uncertain because of conceptual and methodological limitations. These limitations cast doubt on, but do not necessarily disprove, systematic relationships inferred from the immuno-taxonomic data (Collins *et al.* 1991*c*; Curry *et al.* 1991).

Genealogical classification and the role of immuno-taxonomy

As Darwin (1859) presciently noted, the aim of taxonomists should be to create classifications that are 'as far as they can be so made, genealogies'. This target is now in sight, using methods by which phylogenetically useful information may be retrieved from genomes and rigorously interpreted (Hillis and Moritz 1990). Work in progress by Cohen, Gawthrop and Cavalier-Smith and by Stark, Thayer and Cohen has shown that such DNA sequence data will indeed provide a genealogical framework for the classification of living brachiopods, serving either to confirm classical morpho-taxonomy (Williams *et al. in* Moore 1965) or to provide novel insights. By contrast, and for reasons detailed below (and see Cohen 1992), immuno-taxonomy as currently practised cannot create a genealogical (i.e. phylogenetic) classification. Instead, the most important role for immuno-taxonomy is to provide the only known method by which the emerging genealogical classification of living brachiopods may, perhaps, be indirectly extended to at least some relatively recent fossils (Collins *et al.* 1991*a*, 1991*b*) or to Recent brachiopods from which DNA is unlikely to be extracted (e.g. empty shells of dead animals).

For immuno-taxonomy to fulfil this useful role, without danger of creating mis-information, it is essential that there should be prior demonstration of a secure correlation between immuno-taxonomic results and those of the DNA-based, genealogical approach. Although it was claimed that a high degree of congruence between the two approaches has already been established (Curry *et al.* 1993), this was based upon DNA divergence estimation between only one pair of species (Cohen *et al.* 1991) using two relatively insensitive methods of analysis (restriction fragment length polymorphism of mitochondrial DNA and allozyme electrophoresis) both of which revealed so much divergence as to be beyond their known regions of reliability (Nei 1987) and one of which is known to have been upwardly biased (Cohen *et al.* 1993). These data cannot validate the proposed relationship.

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Nevertheless, given that a potentially useful role for the immuno-taxonomy of brachiopods can be envisaged, and even if this role is rejected in favour of it serving merely as a phenetic character that reflects the dubious entity 'gross molecular similarity' (Curry *et al.* 1993), the methodology should be applied and presented in a way consistent with normal practice and with known limitations (Friday 1980; Maxson and Maxson *in* Hillis and Moritz 1990). The discussion which follows highlights some areas in which brachiopod immuno-taxonomy appears to depart both conceptually and methodologically from normal practice.

Independent verifiability

Independent confirmation of the immunological results requires microtitre plate-reading equipment and immunochemical techniques that are not commonly available to taxonomists, together with the successful preparation of suitable antibodies that, as biological reagents, are inherently unpredictable. Also, the requirement for reciprocal antigen–antibody reactions (antibody anti-A versus antigen B and antibody anti-B versus antigen A) means that data-collection cannot be approached piecemeal. For each taxon to be investigated an antibody must be raised by the immunization, with suitable antigen, of a group of experimental animals of the same genetic constitution. The cross-reactivity of each antigen and antibody must then be measured in every possible pairwise combination of antigen–antibody reaction, both homologous and heterologous. Therefore, a complete collection of shells must be amassed, antigen prepared from them all, and the immunizations carried out more-or-less simultaneously. Thus, independent verification of brachiopod immuno-taxonomy is subject to practical barriers.

Nature of the antigens and the concept of Immunological Distance

The brachiopod shell antigens are said to be predominantly carbohydrate and, as soluble extracts of shells (Collins *et al.* 1991*b*), they must be complex mixtures (with one exception, see below). But normal immuno-taxonomy requires protein antigens since carbohydrate epitopes lack phylogenetic significance (Zuckerkandl and Pauling 1965; Cohen 1992). Moreover, the antigens should be homologous and available as purified preparations, as in the widely-exploited cases of serum albumin and lysozyme (Maxson and Maxson *in* Hillis and Moritz 1990). If complex mixtures of antigens are used to raise antisera, analysis becomes uncertain unless, fortuitously, one is immunodominant. Furthermore, in reporting immuno-taxonomic results, the logarithmic transformation of antibody titres to Immunological Distances (ID) is justified only by the empirical correlation between number of aminoacid replacements and ID in specific proteins and may not be appropriate for other types of antigen (Friday 1980; Maxson and Maxson *in* Hillis and Moritz 1990). Therefore both the nature of the antigens and the index used to report the quantitative results involve significant departures from immuno-taxonomic norms. Moreover, because of the chemistry of the brachiopod antigens, the results may even be misleading (Zuckerkandl and Pauling 1965; Cohen 1992).

Character homology

Characters in both phenetic and phylogenetic taxonomy should invariably be homologous. Since, with one exception, shell secondary-layer fibre or whole shell powder extracts served as antigen source (Collins *et al.* 1988, 1991*c*), homology depends on the presence in these diverse shells of an immuno-dominant antigen that is functionally and evolutionarily conserved. However, direct evidence against full homology of shell proteins amongst the taxa analysed exists; a specific chromoprotein (Cusack *et al.* 1992) is present in red brachiopod shells and, by implication, absent from others. Biochemical evidence of antigen homology might have been obtained by immuno-electrophoresis or immuno-blotting, which can be used to characterize antibody and antigen complexity and specificity, but such results were not reported. Thus, brachiopod shell antigen homology remains only an assumption.

Data heterogeneity

For one brachiopod species the antigen was a purified protein, but for all other species it was a whole-shell or shell-fibre extract (Collins *et al.* 1988, 1991*c*; Curry *et al.* 1991). Yet the results obtained with both types of resultant antibody (and both types of antigen) have been combined in a single distance matrix and related cluster analyses as if they were strictly comparable data (Collins *et al.* 1991*c*). This appears to be a substantial departure from normal practice.

Independent variation of antigen concentration and cross-reactivity

Normally, to measure differences in antigen cross-reactivity, a standardized quantity of antigen is added to each test. In the brachiopod cross-reactivity tests, antigen quantity was standardized by the mass of shell from which the tested volume of extract was derived, not by actual antigen quantity, there being no independent assay method. Thus, variation in the concentration of antigen-in-shell and variation in cross-reactivity may both contribute to the immuno-distance estimates. Depending on technique, the initial, antigen-coating stage of the ELISA reactions may provide an escape from this difficulty, but no details were given. Alternatively, it could be assumed that the concentration of antigen in the various samples is reasonably constant, but since one of the antigen samples was a purified protein whose concentration was standardized by a different criterion (Collins *et al.* 1991*c*), this assumption cannot apply. Thus, as well as combining heterogeneous data, the reported ID values confound two potentially independent variables.

Repeatability and reciprocity

It is customary, before basing new taxonomic work on novel quantitative data, to demonstrate that the measurements have desirable statistical properties such as repeatability and, in the case of reciprocal immuno-distance, acceptably small deviations from reciprocity (typically about 2 ID units – Maxson and Maxson *in* Hillis and Moritz 1990). In brachiopod immuno-taxonomy, standard deviations for non-reciprocal assays with three antibodies have been reported (Collins *et al.* 1988), but these relate to data expressed by a different index of cross-reactivity and cannot be applied to ID estimates. In the only reference to reciprocity differences of ID values it is stated that those observed would disrupt only more specific conclusions than were presented (Curry *et al.* 1991). Thus, for the principal brachiopod immuno-taxonomic data (Collins *et al.* 1991*c*; Curry *et al.* 1991), neither summary statistics nor the normal assessment of non-reciprocity (per cent standard deviation – Maxson and Maxson *in* Hillis and Moritz 1990; Hass and Maxson 1992) have been published.

In the absence of relevant statistical analysis two estimates of immuno-distance repeatability may be extracted from the published ID matrix, as follows.

(1) Divergence estimates between a distant outgroup and each member of an ingroup set may be treated as replicates because they effectively measure the same evolutionary relationship. Two independent sets of such comparisons are given (Curry *et al.* 1991, table 1) and summary statistics calculated from these data are: *Mercenaria* – ingroups mean ID = 342·27, SD = 84·84; *Notosaria* – ingroups mean ID = 281·20, SD = 81·65. A very large range of ID values lie within ±2 SD around these means, suggesting either that repeatability is low or that immuno-distance is not closely related to evolutionary divergence. However, this calculation may be inappropriate if experimental errors of log-transformed immuno-distances are not normally distributed.

(2) When the IDs between a distant outgroup and two or more *closely-related* ingroups are determined, the outgroup–ingroup distances should more certainly be identical within experimental error. For the remote rhynchonellid outgroup *Notosaria* and the closely-related terebratulid ingroups *Gryphus* and *Liothyrella*, IDs are given as *Notosaria–Gryphus* 188, *Notosaria–Liothyrella* 324 (Curry *et al.* 1991, table 1). These very different values do fall within the large ±2 SD overlap

noted above, but a more appropriate statistical test might separate them. Either way, they raise questions about reliability of the method.

Conclusion

Immuno-taxonomy of brachiopod shell antigens has a potentially important role in the extension of genealogical classification to fossils and empty shells, but in its current state departs in several important respects from immuno-taxonomic norms. Whilst departures from normal practice may reflect useful innovations, that is hardly so in this case. In consequence, the practical utility of the approach will remain in doubt until it (a) can be conducted with purified, homologous antigens, preferably with aminoacid epitopes, (b) has been calibrated against genomic divergence, (c) has been demonstrated to be satisfactorily repeatable and reciprocal, (d) has been shown to be unconfounded by variation in the concentration of antigen-in-shell, and (e) has been independently confirmed. Thus, to advocate it as a practical approach and basis for new palaeontological work (Curry *et al.* 1993) appears premature.

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Some of the issues raised here have been mentioned in a further account of immuno-taxonomic data which appeared whilst this paper was in press (Endo *et al.*, 1994).

REFERENCE

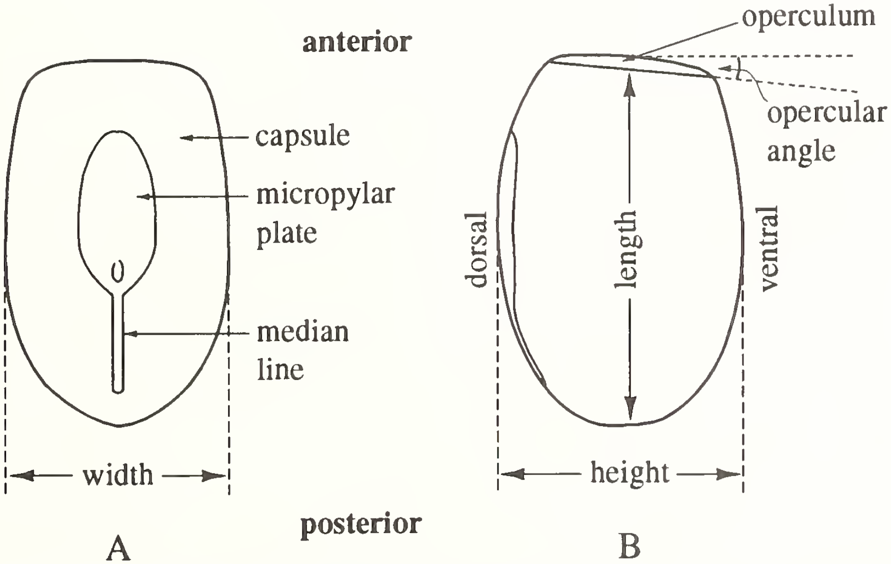
ENDO, K., CURRY, G. B., QUINN, R., COLLINS, M. J., MUYZER, G. and WESTBROEK, P. 1994. Re-interpretation of terebratulide phylogeny based on immunological data. *Palaeontology*, **37**, 349–373.

PHASMIDA (STICK INSECT) EGGS FROM THE EOCENE OF OREGON

by J. T. CLARK SELLICK

ABSTRACT. Three new taxa of fossil stick insects *Eophasma oregonense*, *E. minor* and *Eophasmina manchesteri*, are named from eggs found in the Eocene of Oregon. They are allocated to the tribe Anisomorphini and are the oldest known members of an extant family of the Phasmida.

THE Phasmida is an order of fossil and living insects which includes the stick insects and leaf insects. About 2000 extant species are known, and include some of the longest (over 300 mm) insect species known, if not the bulkiest. Their eggs are unique in possessing both a detachable anterior operculum and, on the dorsal surface, a distinct area of material constituting the micropylar plate. It has been indicated elsewhere (Sellick 1980) that this plate serves both as a location for the micropyles which carry the sperm, and as a respiratory area. It has also been shown that the combination of details of egg capsule and micropylar plate shape is characteristic of various subgroupings within the Phasmida. The eggs show a strong mimicry of plant seeds, which was thought originally to be only in shape. However, it has recently been shown also to extend in capitulate eggs to mimicry of elaiosomes, causing the eggs to be buried by ants in the same way as they treat seeds (Compton and Ware 1991; Hughes and Westoby 1992). The standard descriptive terminology for eggs of the Phasmida (Clark 1976) is illustrated with reference to an egg of the extant genus *Anisomorpha* (Text-fig. 1).



TEXT-FIG. 1. Terminology for the description of eggs of Phasmida (Anisomorphini). A, dorsal, and B, lateral views. The term 'egg' refers to the whole structure, and 'egg capsule' is the coating of the main part of the egg, excluding the operculum. The capitulum, not present on Anisomorphini eggs, is a raised structure on the operculum.

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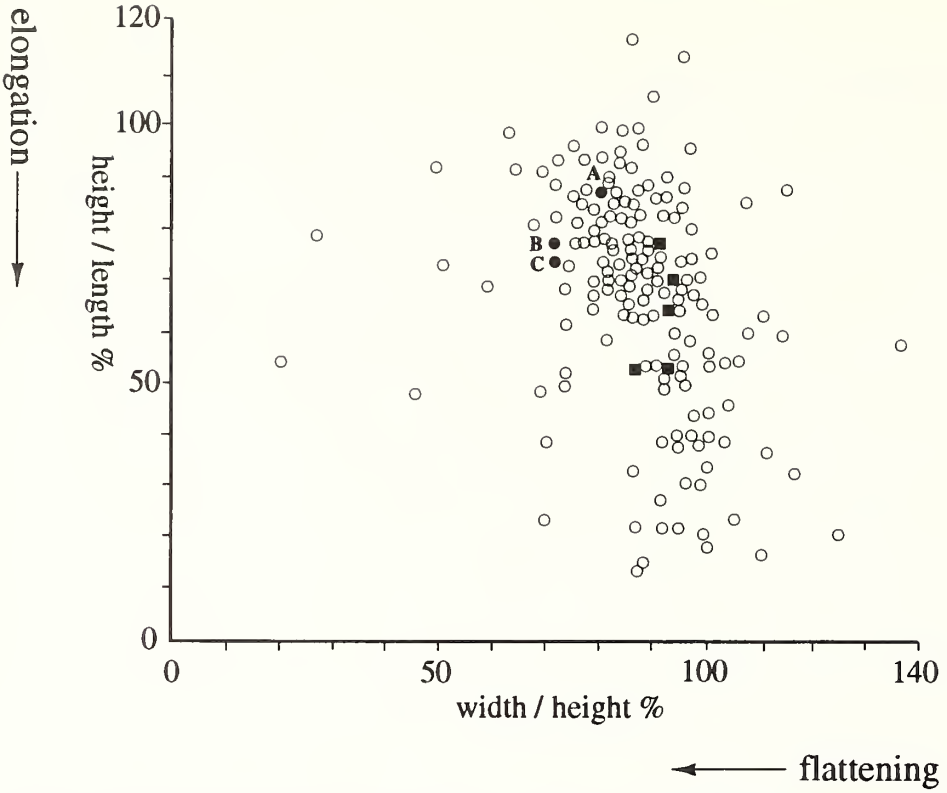
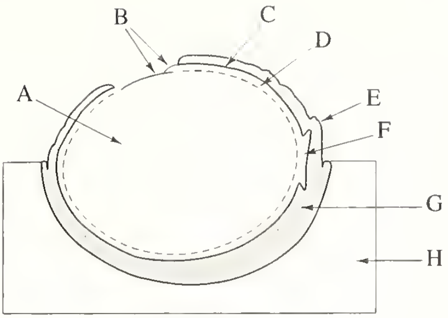


TEXT-FIG. 2. Shape distribution in known eggs of Phasmida. Black circles indicate fossil material: A, *E. oregonense*; B, *E. minor*; C, *E. manchesteri*. Black squares – extant Anisomorphini species; open circles – other known extant species.

The author was recently sent a series of small fossils from the Eocene Clarno Formation of Oregon, which were thought originally to be seeds. The fossils (around 3–4 mm in length) are completely replaced by silica, and preserve a reasonable amount of internal detail. In particular, they show that there is an internal micropylar plate. As in most modern phasmid eggs, the external plate is only slightly raised and can therefore only vaguely be delineated on the surface of the 'seed', and the internal plate was recognized only when the fossils were split parallel to their surface (Text-fig. 3). From this it is evident that the fossils are undoubtedly the remains of eggs of Phasmida and are the only known fossil eggs of this insect order.

Ten well-preserved specimens have been examined and it is concluded that they represent three species within two genera. All have a relatively generalized shape (Text-fig. 4), and are similar in capsule details, having a relatively small micropylar plate with a distinct median line extending posteriorly. Both genera show a feature unusual in extant phasmid eggs of having the operculum tilted ventrally, i.e. having a negative opercular angle. This is known only from a few extent genera, such as *Anisomorpha* and other members of the tribe Anisomorphini. However, the two fossil genera can quite clearly be distinguished from extant ones by details of the opercular structure.



TEXT-FIG. 3. Nature of the fossil material based on a section through *Eophasma oregonense* (UF 225–8686). A, pale silica infilling of egg capsule; B, inner layers seen due to surface fractures; C, outer surface of visible fossil, which is actually a fracture surface within capsule wall; D, inner capsule layer discernible in silica; E, indications of micropylar sculpturing; F, internal micropylar plate; G, full egg capsule wall replaced by dark mineral matter, probably carbonaceous remains of the original organic material permeated by silica; H, outer rock matrix.

MATERIALS AND METHODS

The fossils originated from the Nut Beds within the Clarno Formation, exposed in the John Day Fossil Beds National Monument, about 3 km east of Clarno, north-central Oregon, USA. The Clarno Formation is a non-marine accumulation of volcanic mudflows, tuffs and lavas. The Nut Beds locality is believed to represent a lake delta deposit. Based on radiometric dating, the age of the Nut Beds is *c.* 44 Ma and is thus middle Eocene (Manchester 1990). The eggs were associated with nuts, seeds and other plant debris. Dr Manchester informs me (*pers. comm.*) that they were obtained by prising out blocks of sediment which were then broken up. Remains were exposed in the matrix when intercepted by the resulting fracture planes. The percussion dislodged the silica casts and moulds from the matrix, sometimes leaving behind the outer wall layers. The internal structure was studied on fracture surfaces that developed during the extraction of the fossils. Further details of the palaeobotany and geology of the Nut Beds are given by Manchester (1981, 1990). The specimens are housed in the Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA.

The dimensions are given in the descriptions, and in Table 1, to the nearest 0·05 mm. In the descriptions, the dimensions given of the egg are with the outermost layer of the capsule stripped off, which is probably not more than 0·10 mm in each case. A fragment embedded in matrix showed a fracture within 0·04–0·10 mm of the surface. In Table 1, therefore, the egg proportions are based on a uniform 0·10 mm being added to each surface. The volume of the eggs was calculated as follows:

$$\text{Volume} = \frac{(\text{length})}{2} \times \frac{(\text{width})}{2} \times \frac{(\text{height})}{2} \times 1{\cdot}33 \times \pi.$$

SYSTEMATIC PALAEONTOLOGY

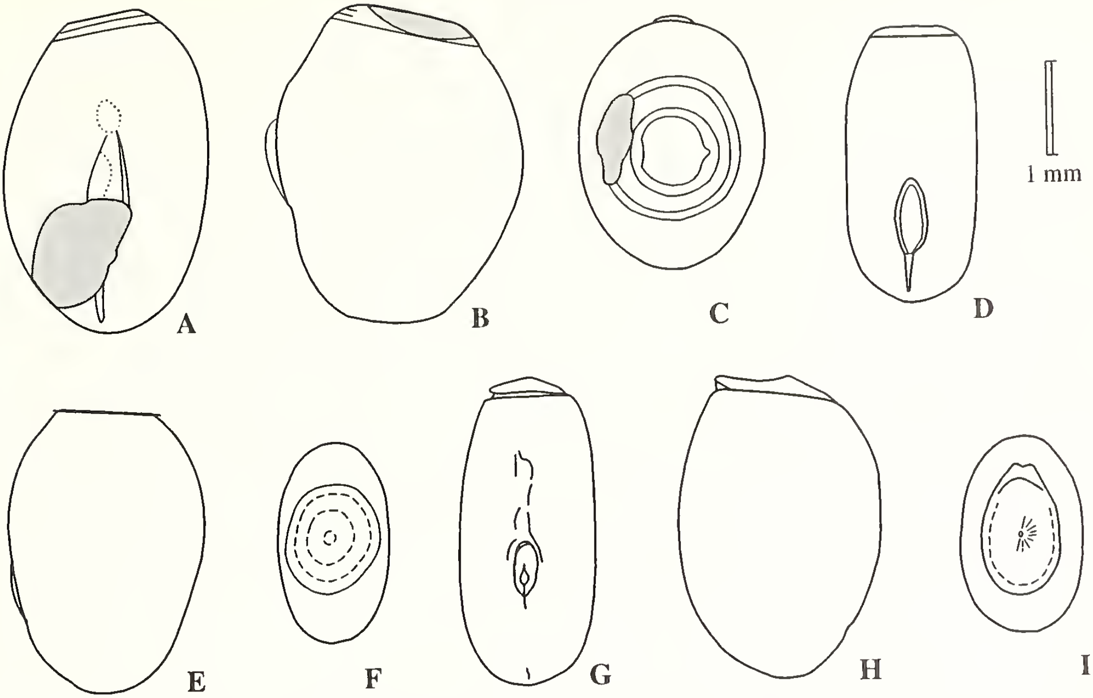
Class INSECTA
Order PHASMIDA Leach, 1814
Family PSEUDOPHASMATIDAE Kirby, 1896
Subfamily PSEUDOPHASMATINAE Kirby, 1896
Tribe ANISOMORPHINI Redtenbacher *in* Brunner von Wattenwyl and Redtenbacher, 1906
Genus EOPHASMA gen. nov.

Derivation of name. Combination of '*Eo*' from Eocene and '*phasma*' from the order name.

Type species. E. oregonense sp. nov.

TABLE 1. Dimensions (in mm) and operculum-type of Phasmida eggs; mpl = micropylar plate length, mpw = micropylar plate width, vol = egg volume (mm^3).

	Length	Width	Height	mpl	mpw	Operculum	w/h %	w/l %	h/l %	Vol
Eophasma oregonense										
UF 15768–6437 (holotype)	3·30	2·25	2·85	1·85	0·50	Ringed	80	72	89	11·1
UF 15768–6364 (paratype)	4·20	2·50	3·10	1·40	0·50	Missing	81	62	76	17·0
UF 15768–6366 (paratype)	3·75	2·40	3·10	1·20	0·60	Missing	78	67	85	14·6
UF 225–8686 (paratype)	3·35	2·45	3·10	—	—	Ringed	79	73	92	13·3
Eophasma minor										
UF 225–8689 (holotype)	3·15	1·55	2·20	1·00	0·35	Ringed	72	53	73	5·6
Eophasmina manchesteri										
UF 15768–6316 (holotype)	3·20	1·50	2·30	0·55	0·25	Conical	68	51	75	5·8
UF 15768–6314 (paratype)	3·10	1·45	2·05	0·50?	0·20	Conical	73	51	70	4·8
UF 15768–6317 (paratype)	2·80	1·50	2·20	0·40?	0·40?	Conical	70	58	82	4·8
UF 225–8688 (paratype)	2·70	1·50	2·00	0·30	0·20	Conical	77	60	78	4·2
UF 15768–6315 (paratype)	2·65	1·35	2·00	0·30	0·25	Conical	70	56	78	3·7



TEXT-FIG. 4. Holotypes of new species of eggs of Phasmida; Nut Beds, Clarno Formation (middle Eocene); John Day Fossil Beds National Park, Oregon, USA. A–C, *Eophasma oregonense* gen. sp. nov.; UF 15768–6437. D–F, *Eophasma minor* gen. et sp. nov.; UF 225–8689. G–I, *Eophasmina manchesteri* gen. et sp. nov.; UF 15768–6316. A, D, G, dorsal views; B, E, H, lateral views; C, F, I, anterior (opercular) views.

Diagnosis. Eggs with roughly lozenge-shaped micropylar plate, in length about one third of capsule length, and with a well defined median line extending towards the posterior pole. Opercular angle negative. Operculum nearly flat with two or three slightly raised concentric rings.

Eophasma oregonense sp. nov.

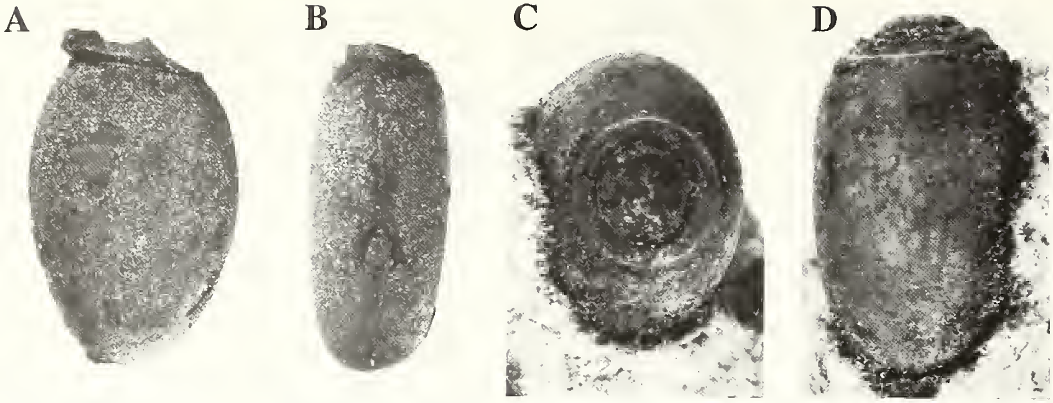
Text-figures 3, 4A–C, 5C–D, 6, 7A–B

Derivation of name. From Oregon, where the fossils were found.

Holotype. UF 15768–6437, from the middle Eocene Nut Beds of the Clarno Formation, John Day Fossil Beds National Monument, north-central Oregon, USA. Paratypes: UF15768–6364, 15768–6366, 225–8686 from the same horizon and locality.

Diagnosis. Eggs with capsule length 3·30–4·20 mm, width 2·25–2·50 mm, height 2·85–3·10 mm. Capsule volume 11·1–17·0 mm^3. Proportions: width/height 79–81 per cent; width/length 62–73 per cent; height/length 76–92 per cent.

Remarks. This is the commoner *Eophasma* species found in the Nut Beds, being represented by four specimens.



TEXT-FIG. 5. Eggs of Phasmida; Nut Beds, Clarno Formation (middle Eocene); John Day Fossil Beds National Park, Oregon, USA; × 12·5. A–B, *Eophasmina manchesteri* gen. et sp. nov.; UF 15768–6316; lateral (A) and dorsal views (B) of holotype. C–D, *Eophasma oregonense* gen. et sp. nov.; UF 225–8686A; anterior (opercular) view (C) and lateral view (D) of specimen before sectioning.

Eophasma minor sp. nov.

Text-figures 4D–F, 7C

Derivation of name. From the small size of the eggs.

Holotype. UF 225–8689, from the middle Eocene Nut Beds of the Clarno Formation, John Day Fossil Beds National Monument, north-central Oregon, USA.

Diagnosis. Egg with capsule length 3·15 mm, width 1·55 mm, height 2·20 mm. Capsule volume 5·6 mm^3. Proportions: width/height 72 per cent; width/length 53 per cent; height/length 73 per cent.

Remarks. Only one specimen of this species was found. It is distinguished from *E. oregonense* by being distinctly smaller, narrower and more elongated.

?Tribe ANISOMORPHINI Redtenbacher *in* Brunner von Wattenwyl and Redtenbacher, 1906
Genus EOPHASMINA gen. nov.

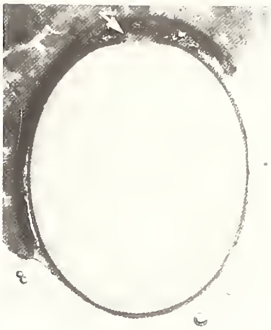
Derivation of name. Diminutive of *Eophasma*.

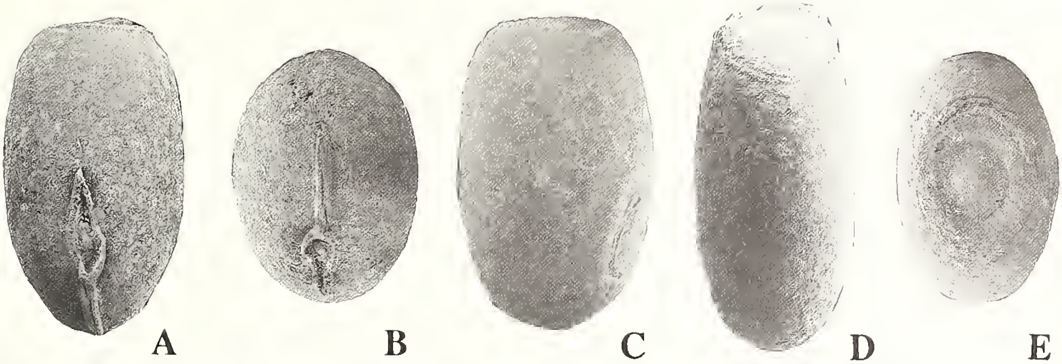
Type species. *E. manchesteri* sp. nov.

Diagnosis. Eggs with small rounded micropylar plate, one sixth or less of the capsule length, and with a less distinct median line than in *Eophasma*. Opercular angle negative. Operculum raised in a shallow cone with a peripheral ring.

Remarks. This genus is distinguished from *Eophasma* mainly by the size and shape of the micropylar plate, the less distinct median line, and the raised operculum. *E. manchesteri* is the commonest species of the phasmid eggs found in the Nut Beds, with five specimens having been found.

TEXT-FIG. 6. *Eophasma oregonense* gen. et sp. nov.; UF 225–8686; Nut Beds, Clarno Formation (middle Eocene); John Day Fossil Beds National Park, Oregon, USA; transverse section through egg, dorsal surface with micropylar plate (arrowed) at top; × 12·5.





TEXT-FIG 7. Eggs of Phasmida, viewed under SEM; Nut Beds, Clarno Formation (middle Eocene); John Day Fossil Beds National Park, Oregon, USA. A–B, *Eophasma oregonense* gen. et sp. nov.; UF 15768–6364; dorsal (A) and dorso-posterior views (B); × 10. C, *Eophasma minor* gen. et sp. nov.; holotype, UF 225–8689; dorso-lateral view; × 12·5. D–E, *Eophasmina manchesteri* gen. et sp. nov.; UF 15768–6315; D, ventral view; × 15. E, anterior (opercular) view; × 16·5.

Eophasmina manchesteri sp. nov.

Text-figures 4G–I, 5A–B, 7D–E

Derivation of name. For Dr Steven Manchester of the University of Florida.

Holotype. UF 15768–6316, middle Eocene, Nut Beds of the Clarno Formation, John Day Fossil Beds National Monument, north-central Oregon, USA. Paratypes: 15768–6314, 15768–6315, 15768–6317, 225–8688, all from the same horizon and locality.

Diagnosis. As for genus.

Dimensions. Capsule length 2·65–3·20 mm, width 1·35–1·50 mm, height 2·00–2·30 mm. Capsule volume 3·7–5·8 mm^3. Proportions: width/height 68–77 per cent; width/length 51–60 per cent; height/length 70–82 per cent.

DISCUSSION

Five small extinct families from the Triassic, Jurassic and Cretaceous, based mainly on wings, together with the extant Phasmatidae and Phylliidae have been attributed to the Phasmida by palaeontologists (Carpenter *in* Kaesler 1992), but entomologists employ a different classification, scope and nomenclature for extant families. The latter is followed here, and the new taxa are included in the Pseudophasmatidae, tribe Anisomorphini, divisions not used by Carpenter.

The oldest previously reported evidence of 'Phasmatidae' *sensu* Carpenter is from the late Eocene (Ross and Jarzembowski 1993). Another early 'phasmatid' (in the palaeontological sense), *Agathamera reclusa* (Scudder), from sediments of probable Miocene age at Florissant, Colorado, USA, is a member of the Anisomorphini. Since the eggs described in the present paper are of middle Eocene age, they would appear to be the earliest record of one of the extant taxa. Nothing is known of the nature of eggs of the extinct families but there is great variation in egg morphology in Recent species, and there is a striking similarity between eggs of *Eophasma* to those of the Anisomorphini. All known eggs of this tribe are non-capitulate and have a marked negative opercular angle, similar to *Eophasma*. The *Anisomorpha* egg similarly also has a small micropylar plate with a distinct median line. The eggs of extant *Agathamera* Stål species have a micropylar plate that runs almost the full length of the capsule and there is no external median line. On balance, I suggest that the evidence supports allocating *Eophasma* to the Anisomorphini.

The eggs of *Eophasma* are clearly non-capitulate (i.e. do not carry a separate structure, a capitulum raised from the operculum). This appears to be a primitive condition, as does the general shape of the egg and the nature of the micropylar plate. In *Eophasmina*, it is possible that the central opercular cone did carry a capitulum, as such cones often do in the eggs of living species. If so, it might indicate that the link between ants and phasmid egg dispersal had developed already by the Eocene. On the other hand, the extant genus *Tectarchus* Salmon of the tribe Hemipachymorphini is unusual in having an egg with a central shallow opercular cone without a capitulum, and it also has a negative opercular angle. Therefore, the existence of a capitulum in *Eophasmina* is not proven. It is believed that the similarity between *Tectarchus* and *Eophasmina* is only superficial, and the latter may be a member of the Anisomorphini.

Acknowledgements. I am grateful to Dr Steven Manchester of the Florida Museum of Natural History for loaning me the material upon which this paper is based, and also for providing me with the scanning electron micrographs used in illustration. Also to Mr A. J. Ross of the Boothe Museum, Brighton, for helping me with the fossil record.

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A NEW DRAGONFLY FROM THE LOWER CRETACEOUS OF BRAZIL

by ANDRÉ NEL *and* FRANÇOIS ESCUILLÉ

ABSTRACT. *Procordulagomphus xavieri* is a new genus and species of gomphid dragonfly (subfamily Cordulagomphinae) from the Lower Cretaceous of Araripe (Brazil). It is the sister-genus of another gomphid from Araripe, *Cordulagomphus*.

THE number of fossil dragonflies known from the Lower Cretaceous Araripe basin increases every year. Carle and Wighton (1990) described two Zygoptera (one Pseudostigmatidae and one Protoneuridae) and six Anisoptera (four Gomphidae and two Aeschnidiidae), while Nel and Paicheler (1994, in press) have described another Gomphidae (*Araripegomphus cretacicus* Nel and Paicheler) and a Corduliidae Gomphomacromiinae (*Araripelibellula martinsnetoi* Nel and Paicheler). Recently, the authors have discovered two new gomphid specimens, that could not be assigned to any described genus and species, and are the subject of the present paper.

The specimens are described using the nomenclature for wing venation proposed by Riek and Kukalova-Peck (1984), which was amended by Nel and Martínez-Delclòs (1993), and Nel *et al.* (1993). The only differences that we add to this nomenclature were suggested to us by Bechly and Jarzembowski (pers. comm.), as follows: RP3/4, for RP3–4 *sensu* Riek and Kukalova-Peck (1984); MAa, for MA1; MAb, for MA2; MPa, for MP1; CuAa, for CuA1; CuAb, for CuA2, and AAa, for AA1 *sensu* Nel and Martínez-Delclòs (1993).

SYSTEMATIC PALAEONTOLOGY

Family GOMPHIDAE Selys Longchamps, 1850
Subfamily CORDULAGOMPHINAE Carle and Wighton, 1990
Genus PROCORDULAGOMPHUS gen. nov.

Derivation of name. From *Cordulagomphus* Carle and Wighton, 1990, the sister-group of this new genus.

Type-species. *Procordulagomphus xavieri* sp. nov.

Diagnosis. Small dragonfly of the Gomphidae, subfamily Cordulagomphinae. Anterior branch MPa of MP joins main branch of MA. Anal triangle lacks cross-vein. Antenodal veins of hind wing fewer and more in line with cross-vein between ScP and RA than in *Cordulagomphus*. RP1 becomes curved at very beginning of pterostigmal brace. Anal loop one-celled. Only three rows of cells in anal and cubito-anal fields. Distal sides (MAb) of discoidal triangles straight. Between RP and MA, before the point of separation of RP3/4, third cross-vein not sigmoid or strongly slanted.

Procordulagomphus xavieri sp. nov.

Text-figures 1–3

1982 'spec. indet., Gomphidae', Schlüter and Hartung, p. 304.

Derivation of name. After our friend Dr Xavier Martínez-Delclòs, in recognition of his numerous studies on fossil insects.

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Types. Female holotype MNHN–LP–R.10406 (Escuillé Collection). Male allotype MNHN–LP–R.10407 (Nel Collection). Specimens stored at the Laboratoire de Paléontologie, Museum national d'Histoire naturelle, Paris.

Type locality and horizon. Nova Olinda, Ceara, Araripe Basin, N.E. Brazil. Crato Formation, Upper Aptian to Lower Albian (Maisey, 1990; Martill, 1993).

Diagnosis. As for genus (this is the only recognized species).

Description of holotype. This is a nearly complete female dragonfly, in which only the legs are missing. The wings are hyaline. The specimen exposes the ventral part of the body.

In the fore wing, the subnodus is not in perfect alignment with the nodus. The nodus is normal, with a well-pronounced nodal furrow. IR1 begins under the proximal part of the pterostigma. The pterostigma covers one and a half cells, and a strongly slanted pterostigmal brace is present. RP1 is curved at the very beginning of the pterostigmal brace. The costal margin and RA are thickened where they border the pterostigma. The arculus is angulate with the lower portion perpendicular to MP+CuA. Sectors of the arculus (RP and MA) are well separated (1·05 mm). Neither Rspl nor Mspl are present. Hypertrigonal, median, submedian, subdiscoidal spaces and discoidal triangle are all free, except for the vein CuP in the submedian space between MP+Cu and AA. Discoidal triangle large and quadrangular; the branch MPa joins the main branch of MA 0·15 mm before MA divides into MAa and MAb at the distal angle of the discoidal triangle. The distal side (MAb) of the discoidal triangle is almost straight. The subdiscoidal space is well-defined, almost triangular in shape. AA divides symmetrically into AA0 (*sensu* Nel *et al.* 1993) and AAa branches. AAa meets CuA exactly at the ventral angle of the discoidal triangle. CuA is never free and separates from MP to meet immediately AAa. The anal field is very simple, with only one row of cells. The cubito-anal field has one and two rows of cells. CuA does not produce a ventral branch. Three rows of cells lie between IR1 and RP2, one row each between RP2 and IR2, RP3/4 and MAa, and MP and CuA. RP3/4 and MAa are straight, but RP2 and IR2 curve slightly to the wing margin. There are six antenodal veins, including AX0. The first three antenodal veins (AX1, AX2 and a third vein) are strongly developed, with the corresponding cross-veins between ScP and RA well in line with them. The two distal antenodal veins are less strongly developed, but still have the corresponding cross-veins between ScP and RA well in line with them. The last antenodal vein is incomplete. The arculus is situated between the two first antenodal veins. There are six postnodal veins, with the cross-veins between RA and RP1 not in line with them. The first postnodal vein is slanted and directed proximally. There is no cross-vein under the first postnodal vein after the nodus. There are only two Bqs between RP2 and IR2 under the subnodus. The fork defined by RP3/4 and RP1/2 is symmetrical. Two cross-veins lie between RP and MA and only one between RP and RA before the fork of RP3/4+RP. There are only three cross-veins between RP and RA, between the arculus and nodus. No supplementary longitudinal vein runs from the distal side (MAb) of the discoidal triangle. Two rows of cells in the postdiscoidal field occur after the discoidal triangle.

Dimensions of fore wing: length 16·6 mm; width at nodus 4·3 mm; base of wing to arculus 2·3 mm; base of wing to nodus 7·5 mm; nodus to apex 9·1 mm; nodus to pterostigma 6·1 mm; pterostigma to apex 2 mm; nodus to arculus 5·2 mm; nodus to RP3/4 2·3 mm; nodus to IR2 1·7 mm; RP2 begins 0·5 mm after subnodus; distance between RA and RP1 just before pterostigmal brace 0·5 mm, just after pterostigmal brace 0·6 mm; an obique vein O is at 1·1 mm from subnodus; pterostigma 1·3 mm long, 0·55 mm wide; distal side of discoidal triangle 1·25 mm long, costal side 1·05 mm long, and proximal side 1·05 mm long; distance between CuA and wing margin 0·6 mm.

The hind wing is almost identical to the fore wing, except for the following points. Only four antenodal veins (the three proximal ones–AX1, AX2 and another vein) are exactly in line with the corresponding cross-veins between ScP and RA. AX2 is the third one. AX2 appears to be a little nearer to the nodus than to AX1. The last antenodal vein is not in line with the corresponding cross-vein between ScP and RA. The arculus is more slightly angulate than in fore-wing. The anal field presents only three rows of cells between AA and the ventral margin. The cubito-anal field also has three rows of nearly regular, hexagonal cells. CuAa has not ventral branch. CuA divides into CuAa and CuAb 0·4 mm from the ventral angle of discoidal triangle. CuAb is well-defined and is directed towards the base of the wing, not towards the ventral wing margin. The one-celled anal loop is well-defined, fully longitudinal, and limited by CuAb and a ventral branch of AA. AA has three short ventral branches. The ventral margin of the wing is rounded at the base. No membranule is present.

Dimensions of hind wing: length 16·5 mm; width at nodus 5·8 mm; base of the wing to arculus 3·0 mm, base of wing to nodus 7·4 mm; nodus to apex 9·1 mm; nodus to pterostigma 5·7 mm; pterostigma to apex 1·7 mm;

TABLE 1. Dimensions of abdomen segments in holotype of *Procordulagomphus xavieri*.

Segment Number	Length (mm)	Width (mm)
10	0·5	1·0
9	0·6	1·5
8	1·4	1·8
7	2·8	3·2
6	3·2	1·6
5	3·5	1·6
4	3·5	1·7
3	3·2	1·8
2	2·0	1·8

TABLE 2. Dimensions of abdomen segments in allotype of *Procordulagomphus xavieri*.

Segment Number	Length (mm)	Width (mm)
10	0·4	1·3
9	1·5	1·5
8	2·0	1·6
7	2·6	1·7
6	2·6	1·1
5	3·2	1·1
4	3·5	1·2
3	3·2	1·2
2	2·0	1·5

nodus to arculus 4·3 mm; nodus to RP3/4 2·2 mm; nodus to IR2 1·6 mm; AX1 to AX2 2·9 mm; AX2 to nodus 2·5 mm; pterostigma 1·8 mm long, 0·7 mm wide; distal side of discoidal triangle 1·8 mm long, costal side 1·7 mm long, proximal side 1·05 mm long; anal loop 1·5 mm long, 0·7 mm wide; AA to ventral margin 2·1 mm; CuA to wing margin 1·9 mm.

The head is 1·8 mm long and 3·5 mm wide, poorly preserved, and visible in section. No detail of dorsal structures can be seen. The eyes seem to be widely separated.

The thorax is 6·2 mm long and 3·5 mm wide, and also preserved in section.

The abdomen is 21·5 mm long and almost complete, although only a part of its internal cuticle is visible. Segment dimensions are given in Table 1. No segments are widened.

The female genital structures are partly preserved at the apex of the abdomen, visible from below. Metagonocoxae extend from middle of segment nine to apex of segment ten. All the ventral surface of segment eight is destroyed.

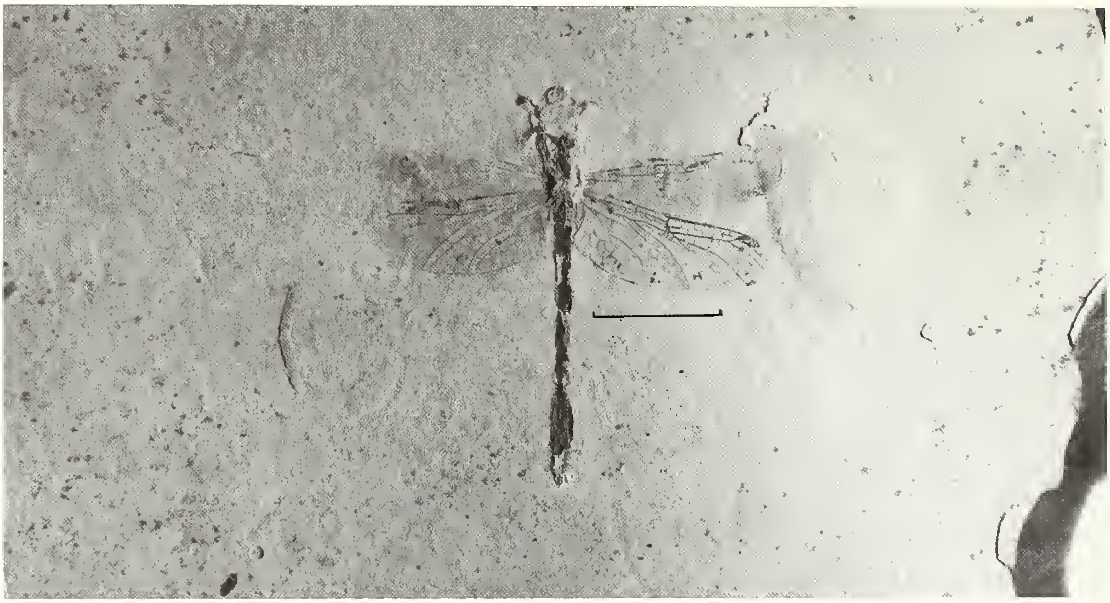
Description of allotype. This is also a nearly complete dragonfly, this time a male, with only the legs, the head and the distal portions of three wings missing. The wings are hyaline. The specimen exposes the ventral part of the body.

The antenodal veins on the fore wing are not well-preserved and the distal parts of wings are missing. The wing is identical to the holotype fore wing except for being smaller.

Dimensions of fore wing: length of preserved part 14·0 mm; width at nodus 4·3 mm; base of wing to arculus 2·5 mm; base of wing to nodus 7·7 mm; nodus to arculus 5·1 mm; nodus to RP3/4 2·3 mm; nodus to IR2 1·6 mm; distal length of discoidal triangle 1·3 mm, costal length 1·0 mm, proximal length 1·0 mm.

The hind wing is identical to that of the holotype, except for its smaller dimensions and the sexual dimorphism structures of the wing base.

The anal loop is also identical to that of the holotype. AA produces only three short ventral branches: one limiting the anal loop, and two proximal branches which rapidly fuse into a straight vein defining the anal



TEXT-FIG. 1. *Procordulagomphus xavieri* gen. et sp. nov. MNHN-LP-R.10407; Nova Olinda, Ceara, Araripe Basin, northeast Brazil; Crato Formation (Upper Aptian to Lower Albian). Scale bar represents 10 mm.

triangle. The ventral wing margin is well angulated. The anal triangle is free of veins; the vein that should in fact be in the anal triangle is fused at its base to the vein that forms the distal side of anal triangle.

Dimensions of hind wing: length 15·6 mm; width at nodus 5·5 mm; base of the wing to arculus 3·0 mm; base of wing to nodus 7·3 mm; nodus to apex 8·3 mm; nodus to pterostigma 5·5 mm; pterostigma to apex 1·8 mm; nodus to arculus 4·4 mm; nodus to RP3/4 2·4 mm; nodus to IR2 1·7 mm; pterostigma 1·7 mm long, 0·6 mm wide; distal length of discoidal triangle 1·7 mm, costal length 1·4 mm, proximal length 1·0 mm; anal loop 1·45 mm long, 0·8 mm wide; anal triangle 2·0 mm long, 1·0 mm wide.

The thorax is nearly 5·0 mm long and 3·2 mm wide, and preserved in section.

The abdomen is 22·4 mm long and almost complete, although only a part of its internal cuticle is visible. Segment dimensions are shown in Table 2.

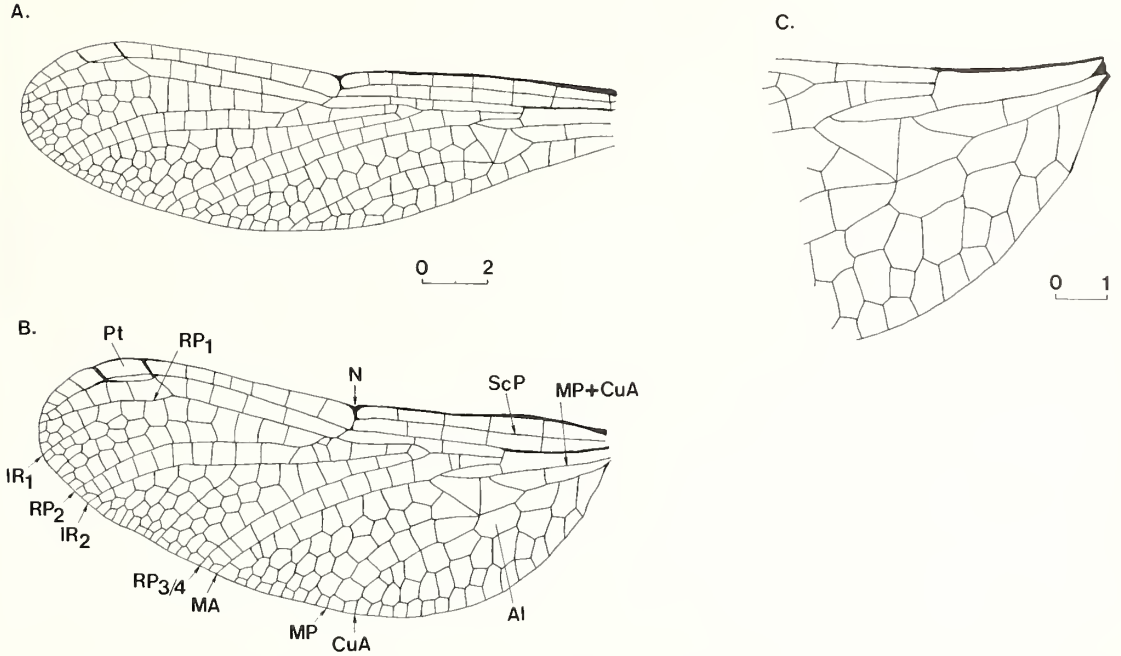
The secondary genital organs are apparently of Neanisopteran type (*sensu* Pfau 1991), and are partly in segment two and partly in segment three. However, the visible structures are almost impossible to interpret. No lateral oreillet is visible.

Two main genital organs ('cerci' *sensu* Aguesse 1968) are visible, 0·9 mm long, but the supra-anal laminae are not preserved.

Discussion. These two specimens, although of different sex, have nearly identical wing structures. The only visible differences (i.e. presence of an anal angle on male hind wing, the female hind wing being basally rounded) reflect sexual dimorphism similar to that found in present-day Gomphidae, and which appeared in early 'Anisozygoptera' and the Anisoptera (Nel *et al.* 1993).

The species is attributed to the Cordulagomphinae as it has all of the wing characteristics of that subfamily, as defined by Carle and Wighton (1990): antenodal veins AX1 and AX2 are present; first postnodal vein slanted with anterior end directed proximally; pterostigmal brace present and strongly slanted; pterostigma short and convex posteriorly; median space free; arculus strongly angulated in fore-wing, more slightly in hind-wing; sectors of arculus widely separated; only three cross-veins between MA and RP before separation of RP3/4; discoidal triangle, hypertrigonal, median, submedian spaces free; anal loop present, longitudinal and well-defined by CuAb and a branch of AA; CuAb directed towards wing base; anal and cubito-anal fields without strong pectinate branches of AA and CuA; anal triangle present in male; membranule vestigial or absent; and female metagonocoxae well developed.

The fossils are very similar in general appearance to the fossil genus *Cordulagomphus* (Text-figs 4–5), also from the Araripe deposits. Of the characters used to distinguish them from *Cordulagomphus*, the following are regarded as apomorphies of *Procordulagomphus*: the anterior branch MPa of MP joins the main branch of MA and not the distal angle of the discoidal triangle; the anal triangle is free of cross-veins; the antenodal veins of the hind wing are fewer and more in line with the cross-veins between ScP and RA; and RP1 is curved from the very beginning of the pterostigmal brace. The following are plesiomorphies of *Procordulagomphus*: the anal loop is one-celled; the anal and cubito-anal fields have only three rows of cells; the distal sides (MAb) of the four discoidal triangles are straight; and the third cross-vein between RP and MA, before the point of separation of RP3/4, is neither sigmoid nor strongly slanted. As the two genera are well-characterized by these characters, *Procordulagomphus* is interprete as a sister-genus of *Cordulagomphus*.

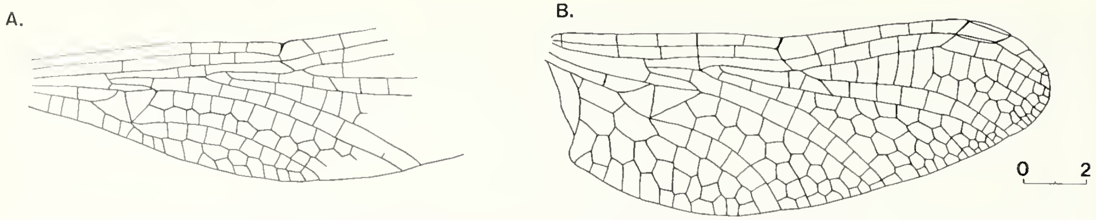


TEXT-FIG. 2. *Procordulagomphus xavieri* gen. et sp. nov. MNHN-LP-R.10406 (holotype). Nova Olinda, Ceara, Araripe Basin, northeast Brazil; Crato Formation (Upper Aptian to Lower Albian). A, fore wing; B, hind wing; C, closeup of base of hind wing. A1, Anal loop; N, Nodus; Pt, Pterostigma. Scale bars in mm.

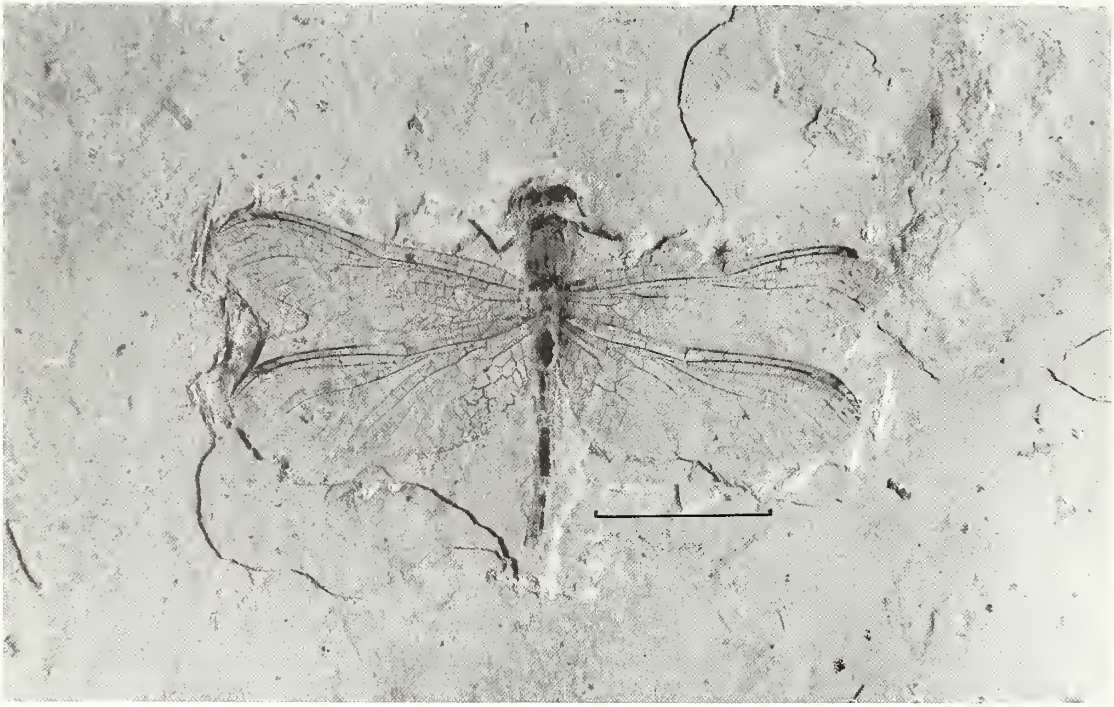
Both *Procordulagomphus* and *Cordulagomphus* are clearly quite different from *Araripegomphus cretacicus* Nel and Paicheler from the same deposits at Araripe, most obviously in being much smaller. According to Nel and Paicheler (1994), *Araripegomphus* does not belong to Cordulagomphinae.

CONCLUSIONS

With the discovery of *Procordulagomphus*, there are now three genera and four species of Gomphidae known from the Araripe palaeolake, where they were obviously well represented. The Cordulagomphinae would appear to have been one of the more diverse groups of dragonflies



TEXT-FIG. 3. *Procordulagomphus xavieri* gen. et sp nov. MNHN-LP-R.10407 (allotype). Nova Olinda, Ceara, Araripe Basin, northeast Brazil; Crato Formation (Upper Aptian to Lower Albian). A, fore wing; B, hind wing. Scale bar in mm.

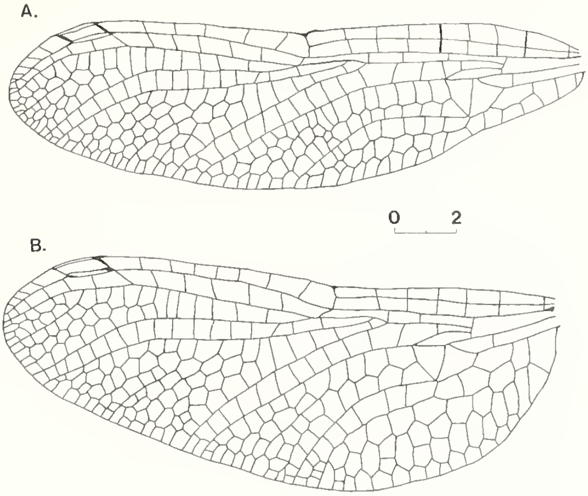


TEXT-FIG. 4. *Cordulagomphus fenestratus* Carle and Wighton, 1990. MNHN-LP-R.10408, female; Nova Olinda, Ceara, Araripe Basin, northeast Brazil; Crato Formation (Upper Aptian to Lower Albian); Scale bar represents 10 mm.

present there, although further evidence of fossil dragonflies from Araripe may require this view to be revised. For instance, the very recent discovery of a new Libelluloidea (Jarzembowski and Nel, work in progress) shows that other taxa are to be found in Araripe's deposits.

Carle and Wighton (1990) suggested that the gomphids of the fossil subfamily Cordulagomphinae may have been adapted to a low-energy environment. This contrast with the present-day gomphids, which tend to be associated with rivers and running water. The habitats of the Cordulagomphinae larvae remain uncertain, even if we now know that the adult stages of those dragonflies were common and diverse in the Araripe palaeolake. Perhaps the Cordulagomphinae larvae lived in streams near the palaeolake and the adults invaded the lake for hunting.

The relationship of the Cordulagomphinae to the other gomphid subfamilies remains unclear (Nel and Paicheler 1994). This is not helped by our knowledge of Mesozoic Gomphidae still



TEXT-FIG. 5. *Cordulagomphus fenestratus* Carle and Wighton, 1990. MNHN-LP-R.10408, female; Nova Olinda, Ceara, Araripe Basin, northeast Brazil; Crato Formation (Upper Aptian to Lower Albian); Scale bar represents 10 mm.

being so poor, with many genera and species needing revision, even including apparently well-known taxa like *Nannogomphus bavaricus* Handlirsch, 1906 (Nel and Martínez-Delclòs, in press; Jarzembowski and Nel, work in progress). Nevertheless, the Brazilian Cordulagomphinae demonstrate that the Gomphidae were already widespread and diverse during the Early Cretaceous. A fascinating and unresolved question is how one of the more diverse and widespread Mesozoic dragonfly families, the Aeschnidiidae, with taxa known from throughout the Early Cretaceous biosphere, became extinct during the middle Cretaceous, while the Gomphidae and other modern Anisopteran groups remained undisturbed. Contingent disappearance could be a convenient answer but it still had to be demonstrated. Further studies on Mesozoic dragonflies are clearly necessary before we are able to answer that problem.

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AN OPLEGNATHID FISH FROM THE EOCENE OF ANTARCTICA

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and DAVID R. BELLWOOD

ABSTRACT. The oldest remains of the teleost family Oplegnathidae are reported from Antarctica. Fragmentary beaks with the typical coalesced teeth have been discovered. The Antarctic material presents characteristic features of members of the extant Oplegnathidae: jaws lacking lateral canines, distinctly crenulate cutting margins, teeth with narrow cutting edges that show evidence of a bipartite structure; there are also large rounded molariform teeth on the medial face of the jaws. This record confirms that the seawater was temperate when rocks of Telms 4–5 (middle Eocene) of La Meseta Formation were deposited. Oplegnathids had at that time a wider geographical distribution than today.

NUMEROUS remains of chondrichthyan and osteichthyan fishes have been recovered from the La Meseta Formation (dated as Eocene by Elliot and Trautman 1982) in the northern part of Seymour Island, Antarctica (e.g. Woodward 1908; Cione *et al.* 1976; Cione 1978; Tonni and Cione 1978; Cione and Reguero 1994, in press; Welton and Zinsmeister 1980; Grande and Eastman 1986; Doktor *et al.* 1988; Eastman and Grande 1991; Jerzmanzska 1991; Long 1991*a*, 1991*b*, 1992).

Researchers from the Departamento Científico Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, with the support of the Instituto Antártico Argentino, have been surveying the Cretaceous and Tertiary rocks of Seymour and other neighbouring islands each summer. During the summers of 1991–2 and 1992–3, the palaeontologist Marcelo Reguero found three jaw fragments in the middle beds of the La Meseta Formation. These fragments appeared to be of an osteichthyan fish with coalesced teeth.

Only a few osteichthyan families have been described with coalesced teeth, namely the Tetraodontidae, Diodontidae, Odacidae, Scaridae, Oplegnathidae, and the fossil Paleolabridae. In the present paper, the Antarctic material is described and its identity discussed in relation to these families. In addition, the biogeographical and palaeoclimatological implications of the find are considered.

LOCALITY AND STRATIGRAPHY

The material was collected from the Eocene of the La Meseta Formation (Elliot and Trautman 1982) in the northern part of Seymour (Marambio on Argentinian maps) Island (64° 14′ S, 56° 43′ W), Antarctica (Text-fig. 1). The La Meseta Formation rests on the Cross Valley Formation or on the Marambio Group (Rinaldi *et al.* 1978; Rinaldi 1982). It consists of 600 m of shallow marine, poorly consolidated sediments. Sadler (1988) subdivided this unit into seven informal lithostratigraphical subunits named Telm 1 to Telm 7. The material comes from the middle part of the formation (Telm 5; Text-fig. 2). Telm 5 comprises well sorted sands, interlaminated sand/mud channel fills, and shelly conglomerates. Selachian teeth are very abundant in Telms 4–5 but rare in Telms 6–7 (Cione *et al.* 1976; Tonni and Cione 1978; Sadler 1988). In contrast, osteichthyan remains are relatively common in Telm 7. In the sand/mud lithofacies of Telm 5, plant remains (Gandolfo *et al.* 1990) are abundant, together with land mammals and marine invertebrates (Zinsmeister 1984; Woodburne and Zinsmeister 1984; Reguero *et al.* 1993). Telms 4–5 were interpreted by Trautman (1976) and Elliot and Trautman (1982) as being deposited in a prograding delta and could represent the

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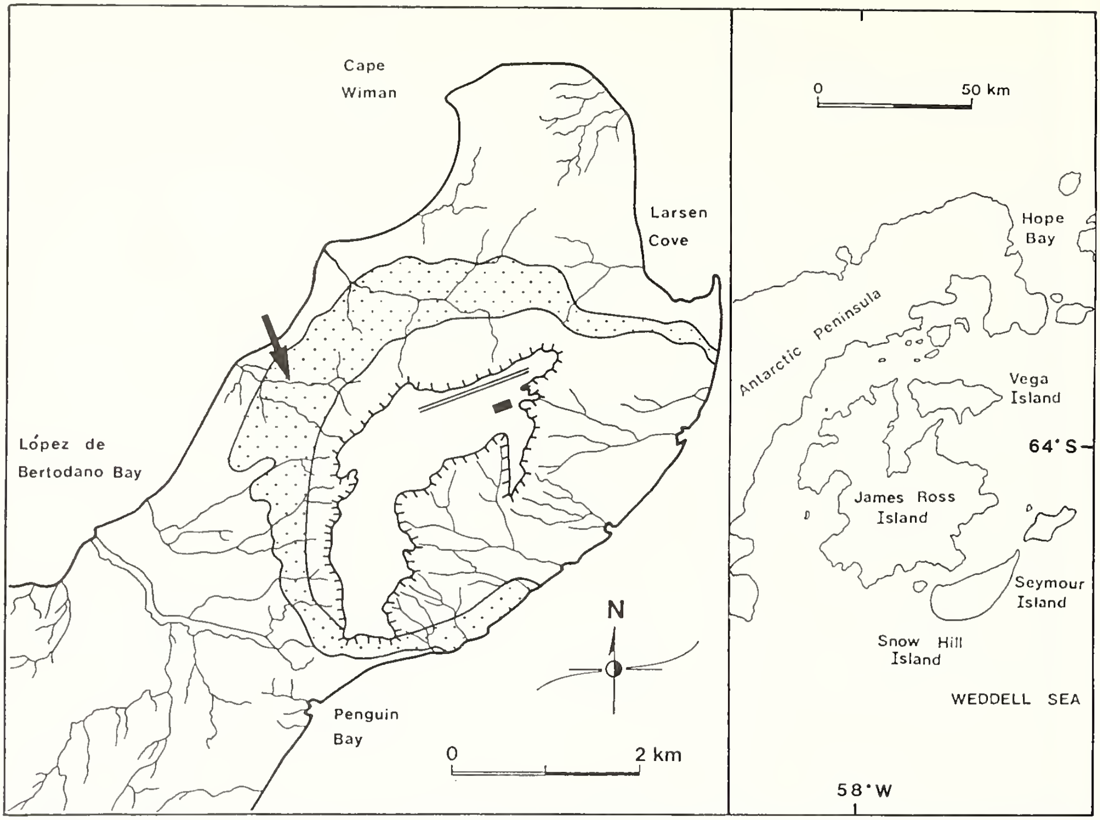


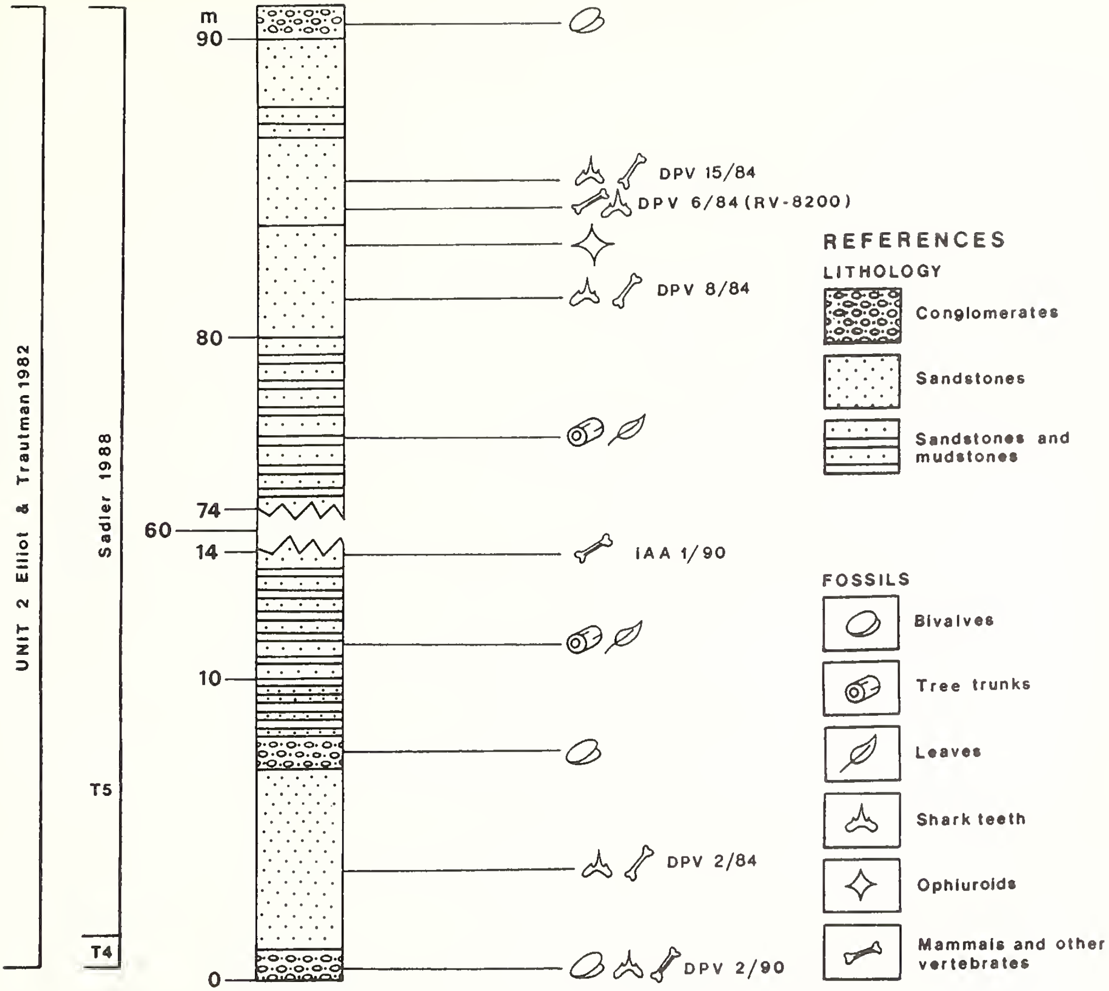
TEXT-FIG. 1. Sketch map to show the Seymour Island location and tip of the island with the outcrops of Telms 4 and 5 of the La Meseta Formation (stippled area). The arrow indicates the collecting locality IAA 1/90.

development of tidal channels and bars and/or spits with a sheltered back bar area. Dinoflagellate cyst, diatom, microplankton, and fish evidence suggest a middle to late Eocene age for Telms 4 and 5 (Wrenn and Hart 1988; Askin *et al.* 1991; Cocozza and Clarke 1992; Cione and Reguero 1994, in press). The mammal assemblage (closely related to South American taxa) indicate a middle Eocene age for Telm 5 (Mustersan in the southern South American standard; Reguero *et al.* 1993; Bond *et al.* 1993).

All material was collected from locality IAA 1/90 (Text-fig. 1) which is about 300 m north-west of locality DPV 6/84 (RV-8200 of Woodburne and Zinsmeister 1984 – the 'Rocket Site', or 'Mammal Site'). It is on an elevation of about 50 m overlooking the coast. This locality is also referred to by some authors as the 'Ungulate Site' because several South American ungulates were found there (Reguero *et al.* 1993; Bond *et al.* 1993; M. Reguero, personal communication). The macrofauna is dominated by naticid gastropods (*Polinices*), whilst bivalves, bryozoans, goneplacid crabs (*Chasmocarcinus seymourensis*), teredid bored wood, leaves, and several trace fossils have also been collected from this locality (M. Reguero, personal communication).

RECENT COMPARATIVE MATERIAL

Oplegnathidae: *Oplegnathus woodwardii* NMV A269; *Oplegnathus conwayi* NMV A712 (NMV – Museum of Victoria, Melbourne, Australia). *Oplegnathus insignis* (Museo Nacional de Historia Natural, Santiago, Chile). Scaridae and Odacidae – registration numbers of most material are given in Bellwood (in press). Odacidae: *Neoodax balteatus* MLP 9086; *Olisthops cyanomelas* MLP 9085.



TEXT-FIG. 2. Stratigraphical section (part of Telm 4 and Telm 5).

Scaridae: *Scarus sordidus* MLP 9087 (Museo de La Plata, La Plata). Additional unregistered material of the Tetraodontidae, Diodontidae, Scaridae, Odacidae, and Oplegnathidae were also examined.

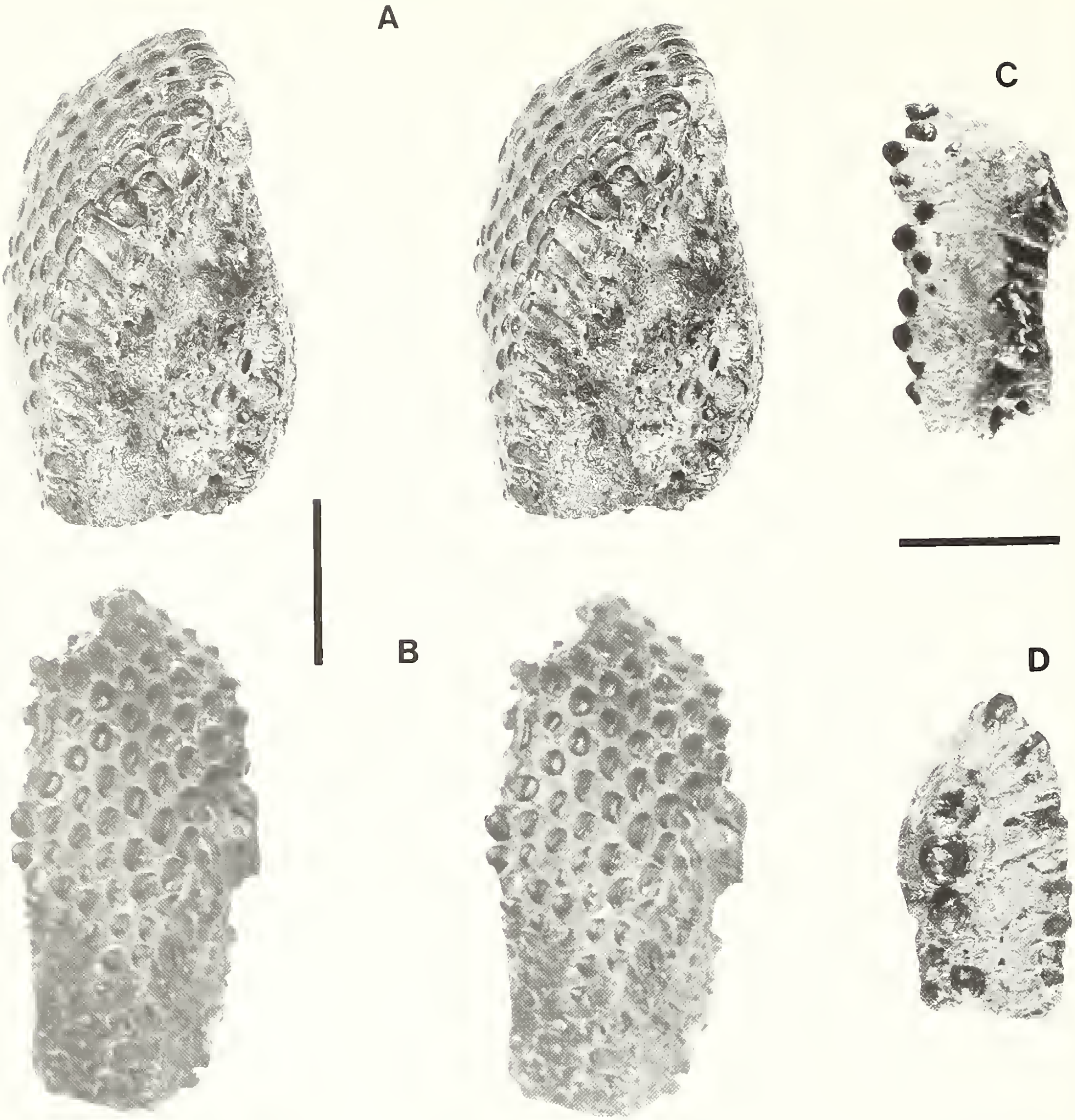
SYSTEMATIC DESCRIPTION

Order PERCIFORMES Muller, 1844
Family OPLEGNATHIDAE Bleeker, 1854
Oplegnathidae indet.
Form A

Text-figures 3A–B, 4

Material. MLP 93-1-6-5. Left premaxilla. All the Antarctic material is deposited in the Departamento Científico Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina (MLP).

Description. The outer surface of the dental plate is nodular, with individual teeth exposed (Text-fig. 3A–B). The exposed face of each tooth consists of two different areas: basal and apical. The apical surface is covered by



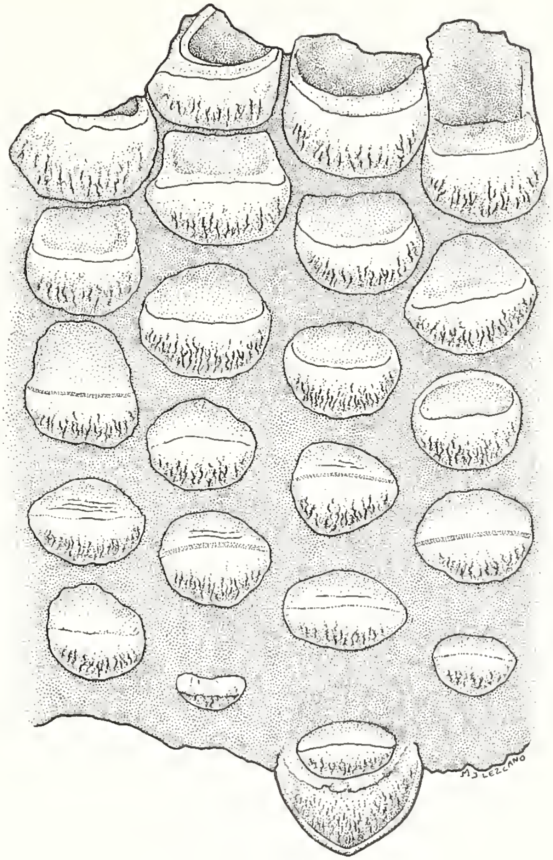
TEXT-FIG. 3. Oplegnathidae indet.; northern part of Seymour Island, Antarctica; Telm 5, La Meseta Formation (Eocene). A–B, Form A; MLP 93-1-6-5; left premaxilla; scale bar represents 10 mm. A, basal view. B, labial view. C–D, Form B; MLP 90-1-20-141; left premaxilla; scale bar represents 5 mm. C, labial view. D, occlusal view.

enameloid with a granular ornamentation. Both surfaces are clearly separated by a shallow sulcus (Text-fig. 4).

The occlusal surface of marginal teeth is rounded in teeth near the symphysis but that of more commisural ones is pointed. There are four complete incisiform teeth in the margin of the plate, while the remaining teeth are damaged. All marginal teeth present a transverse, sharp cutting edge. The basal boundary is rounded when complete (Text-fig. 4). Tooth rows are clearly recognizable and somewhat imbricate.

The outer series of teeth seems to be followed by a smaller inner series, near the symphysis; the symphysis is partially occupied by four strongly imbricated rectangular teeth. In addition, a few molariform teeth are

TEXT-FIG. 4. Oplegnathidae indet., Form A; MLP 93-1-6-5; northern part of Seymour Island, Antarctica; Telm 5, La Meseta Formation (Eocene); left premaxilla, detail of the labial surface.



located on the lingual side of the dental plate, below the cutting margin of the jaw. Canines are not visible. The symphysis is broad and plain.

Form B

Text-figure 3C–D

Material. MLP 90-1-20-141, jaw fragment. MLP 91-11-4-208, jaw fragment.

Description. MLP 90-1-20-141 is almost complete. The outer surface of the dental plate is smooth (Text-fig. 3C). Individual teeth (ten) are exposed only on the margin. Six teeth are completely erupted. The teeth are flattened, with a transverse cutting edge. The enamel is granular in appearance. A row of four large molariform teeth is located on the lingual face of the dental plate (Text-fig. 3D). These teeth are larger than the teeth in the dental plate. The second specimen (MLP 91-11-4-208) is fragmentary but is comparable to this form.

Although two forms are described, they may belong to different ontogenetic stages as the material appears to correspond to medium (Form B) and large (Form A) individuals.

ADDITIONAL FOSSIL MATERIAL OUTSIDE ANTARCTICA

There are a number of published records and additional undescribed fragments that bear a strong resemblance to the material described above. They are also provisionally referred to the Oplegnathidae (following Bellwood and Schultz 1991), although the fragmentary nature of the material means that any such designation must be tentative.

Chapman and Cudmore (1924) described the oplegnathid *Oplegnathus manni* from the Kalimnan formation (lower Miocene) of Victoria, Australia. *Scarus baltringensis* Probst, 1874 (also Wittich 1898), *Scarus priscus* Wittich, 1898, and *Scarus suevicus* Probst, 1874 are all based on dental plate fragments and all appear to be referrable to the Oplegnathidae (*cf.* Bellwood and Schultz 1991). All are from northern Europe, the two former '*Scarus*' species being recorded from Oligocene deposits (Wittich 1898).

Undescribed additional material. BMNH P38006 – Left premaxilla, Sharktooth Hill, Kern County, California, USA (Miocene); BMNH P13933, 13934, 9737 – dental plate fragments, Kalimnan, Beaumaris, Melbourne, Australia (Miocene) (BMNH – Natural History Museum, London, UK).

DISCUSSION

Systematic status

Of the six families reported with coalesced teeth, the material clearly differs from beaks of the families Odacidae, Tetraodontidae, Diodontidae, and the extinct Paleolabridae, by the presence of large rounded molariform teeth on the medial face of the jaws (see Boas 1879; Estes 1969; Britski *et al.* 1985; Gomon and Paxton 1985). In addition, in the tetraodontids and diodontids, the teeth are completely covered by an enameloid layer with no individual teeth erupting on the cutting edge, whilst the teeth of odacids are small, conical, and tightly imbricated (Gomon and Paxton 1985).

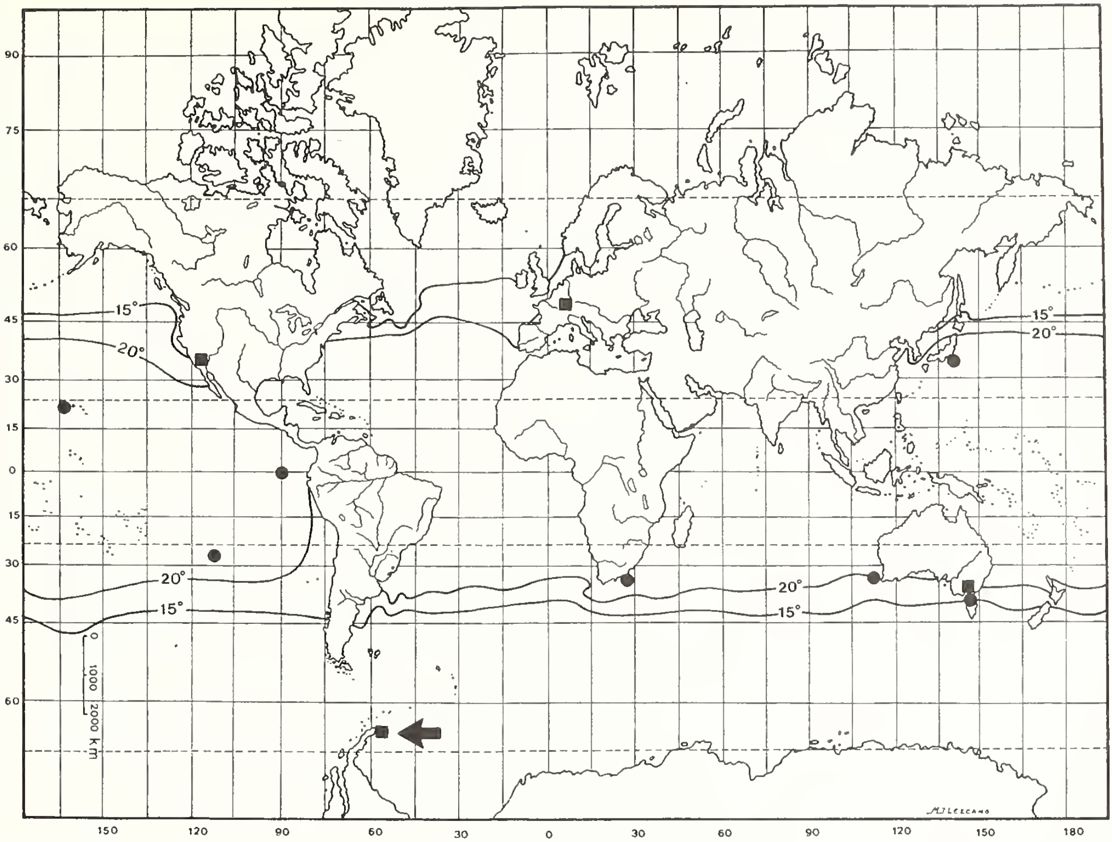
The two remaining families with coalesced teeth, the Scaridae and Oplegnathidae, both have representatives with molariform teeth on the medial face of the jaws (Bellwood and Schultz 1991; Bellwood, in press). However, the Antarctic material differs from extant scarids in several respects. The material may be distinguished from the genera *Cryptotomus*, *Nicholsina*, *Calotomus*, *Leptoscarus*, *Hipposcarus* and *Scarus* by the shape of the teeth and the absence of lateral canines (present in all but a few *Scarus* species). Of the extant scarids, the material most closely resembles the genera *Chlorurus*, *Bolbometopon*, *Cetoscarus* and *Sparisoma*, which share the crenate cutting edge and may lack lateral canines. Of these, however, only some *Sparisoma* species have molariform teeth on the medial face of the jaws. The material differs from *Sparisoma* and all other scarids in the form of the teeth with the distinct bipartite structure. In addition, the medial molariform teeth of *Sparisoma* are smaller than in the Antarctic material and most *Sparisoma* species have lateral canines.

In contrast, the form of the Antarctic material is entirely consistent with that of extant members of the Oplegnathidae. In the Oplegnathidae, the jaws lack lateral canines and have a distinctly crenate cutting margin, whilst the teeth have a narrow cutting edge and may show evidence of the bipartite structure; there are also large rounded molariform teeth on the medial face of the jaws.

At present, there are no dental synapomorphies available with which to positively identify a member of the Oplegnathidae, nor is the material sufficient to provide a robust identification. However, the features of the material available are, in all respects, comparable to those of Recent Oplegnathidae and the specimens are therefore provisionally placed in this family.

Biogeographical notes

This is the first record of an oplegnathid from Antarctica and the oldest known in the world. Its occurrence in the Antarctic Peninsula is not surprising considering their widespread present-day distribution in warm-temperate seas (Japan, western Australia, Tasmania, Hawaii, Easter and Galapagos islands, and South Africa; Text-fig. 5) and that temperate sea water was present off the Antarctic Peninsula when Telms 4–5 beds of the La Meseta Formation were deposited (Cione *et al.* 1976; Cione 1978; Tonni and Cione 1978; Cione and Reguero 1994, in press). This observation is



TEXT-FIG. 5. Distribution of the Family Oplegnathidae. The arrow indicates Seymour Island. Isotherms of 15 °C and 20 °C for February (southern Hemisphere) and August (northern Hemisphere) are depicted (according to Sverdrup *et al.* 1942). Squares represent fossil records and circles indicate recent reports.

further supported by the high frequency of occurrence of the sharks *Carcharias*, followed by *Squatina*, *Pristiophorus*, *Isurus*, and the skate *Myliobatis* (Cione *et al.* 1976; Cione 1978; Welton and Zinsmeister 1980; Long 1992). Recent representatives of these taxa are common in temperate seas (Cione 1978; Compagno 1984).

The age and locations of the fossil oplegnathids point to a widespread distribution during the early Cenozoic. This was followed by a contraction of the geographical range of the family, as evidenced by the absence of Recent representatives from both the Atlantic and Pacific coasts of North America. Both locations have fossil records of the family, with middle Miocene material from the west coast of North America pointing to a relatively recent loss of the family from this area. The timing of the loss from the Atlantic Ocean is unknown (except post-Oligocene in Europe). However, the extirpation of this family from the Antarctic Peninsula is probably associated with the drop of marine temperatures detected through the Telms 4–5 (middle Eocene) to Telms 6–7 (upper Eocene) in the La Meseta Formation (Cione 1978; Tonni and Cione 1978; for additional data on global climatic changes during the Eocene-Oligocene, see Frakes *et al.* 1992; Prothero and Berggren 1992). Why the family should be lost from the Atlantic, where warm-temperate waters could be found throughout the Cenozoic, is less clear. A similar reduction or extirpation from the Atlantic Ocean is known for the sharks *Heterodontus* and *Pristiophorus*. *Heterodontus* is common in Oligocene and Miocene beds in Patagonia and central Argentina (Ameghino 1906; Cione 1978). *Pristiophorus* occurs in the Eocene to Pliocene of Europe, the Oligocene and Miocene of Patagonia, and also in the Eocene of Seymour Island (see Cione 1988; Cione and Expósito 1980; Grande and Eastman 1986). Only an endemic species, *Pristiophorus schroederi* Springer and Bullis, 1960 persists in the Bahamas region, western North Atlantic (Compagno 1984).

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THE SKULL OF THE CALLOVIAN PLESIOSAUR *CRYPTOCLIDUS EURYMERUS*, AND THE SAUROPTERYGIAN CHEEK

by DAVID S. BROWN *and* ARTHUR R. I. CRUICKSHANK

ABSTRACT. Mechanical preparation of a relatively complete new skull specimen of *Cryptoclidus eurymerus* has revealed the palate and cheek regions for the first time, permitting a more accurate reconstruction to be given. The wider phylogenetic implications of differing cheek and orbit configurations in sauropterygians are discussed and a cladogram given: the Cryptoclididae and the remaining plesiosauroids are sister groups; deep ventral cheek excavation arose through loss of the diapsid lower temporal arch and is a shared derived character of cryptoclidids, whereas an enlarged orbit and narrow vertical jugal bar are apomorphies. The palatal and mandibular structure of *Cryptoclidus* is derived in comparison with pliosauroids: coronoids, prearticulars, suborbital fenestrae and the large pterygoid flange are all absent. These differences relate to feeding habit: *Cryptoclidus* fed on small soft-bodied prey, and shows no adaptations for resisting torsional forces upon the jaws. Underwater olfaction similar to the pliosauroid system may have been present in *Cryptoclidus*.

THE structure of the skull in plesiosauroid specimens from soft clays is often deficient in delicate areas due to poor preservation, rough collection and subsequent handling. In particular, the cheek and skull roof of the Callovian genus *Cryptoclidus* from the English Lower Oxford Clay have of necessity been reconstructed from deficient specimens (Andrews 1910; Brown 1981*b*).

On 4th September 1987 a new and almost complete specimen of *Cryptoclidus eurymerus* was discovered at Dogsthorpe, near Peterborough, UK (Martill 1988). The skull was collected in a moist clay block supported by a plaster jacket, and was then removed to the laboratory of Leicestershire Museum and Art Gallery. The plaster jacket was replaced by a double-sided silicone rubber support, and the specimen was prepared (by A.R.I.C.) using mechanical methods including an 'Airbrasive' machine. Breaks were repaired with acetone-soluble plastics. Although nevertheless distorted and incomplete due to post mortem crushing and drop-out, the specimen is the best known skull of *Cryptoclidus*.

SYSTEMATIC PALAEONTOLOGY

Abbreviations used. BMNH, Palaeontology Collections, Natural History Museum, Cromwell Road, London SW7 5BD. Previously the British Museum (Natural History). PETMG, Geological Collections, Peterborough City Museum and Art Gallery, Priestgate, Peterborough PE1 1LF.

Subclass SAUROPTERYGIA Owen, 1860
Order PLESIOSAURIA de Blainville, 1835
Superfamily PLESIOSAUROIDEA (Gray, 1825) Welles, 1943
Family CRYPTOCLIDIDAE Williston, 1925

Diagnosis. See Brown (1994).

Genus CRYPTOCLIDUS Seeley, 1892

Type species. Cryptoclidus eurymerus (Phillips, 1871) from the Lower Oxford Clay of Peterborough, UK.

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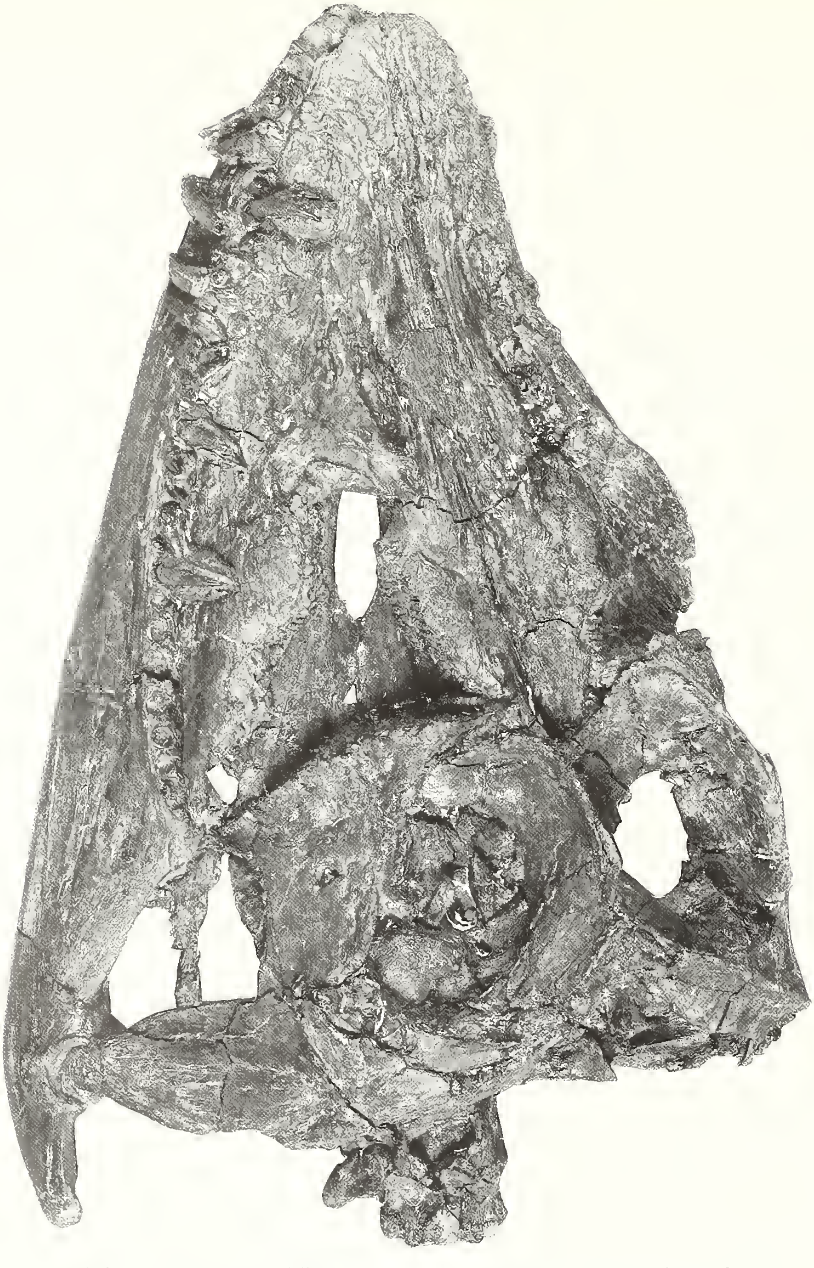


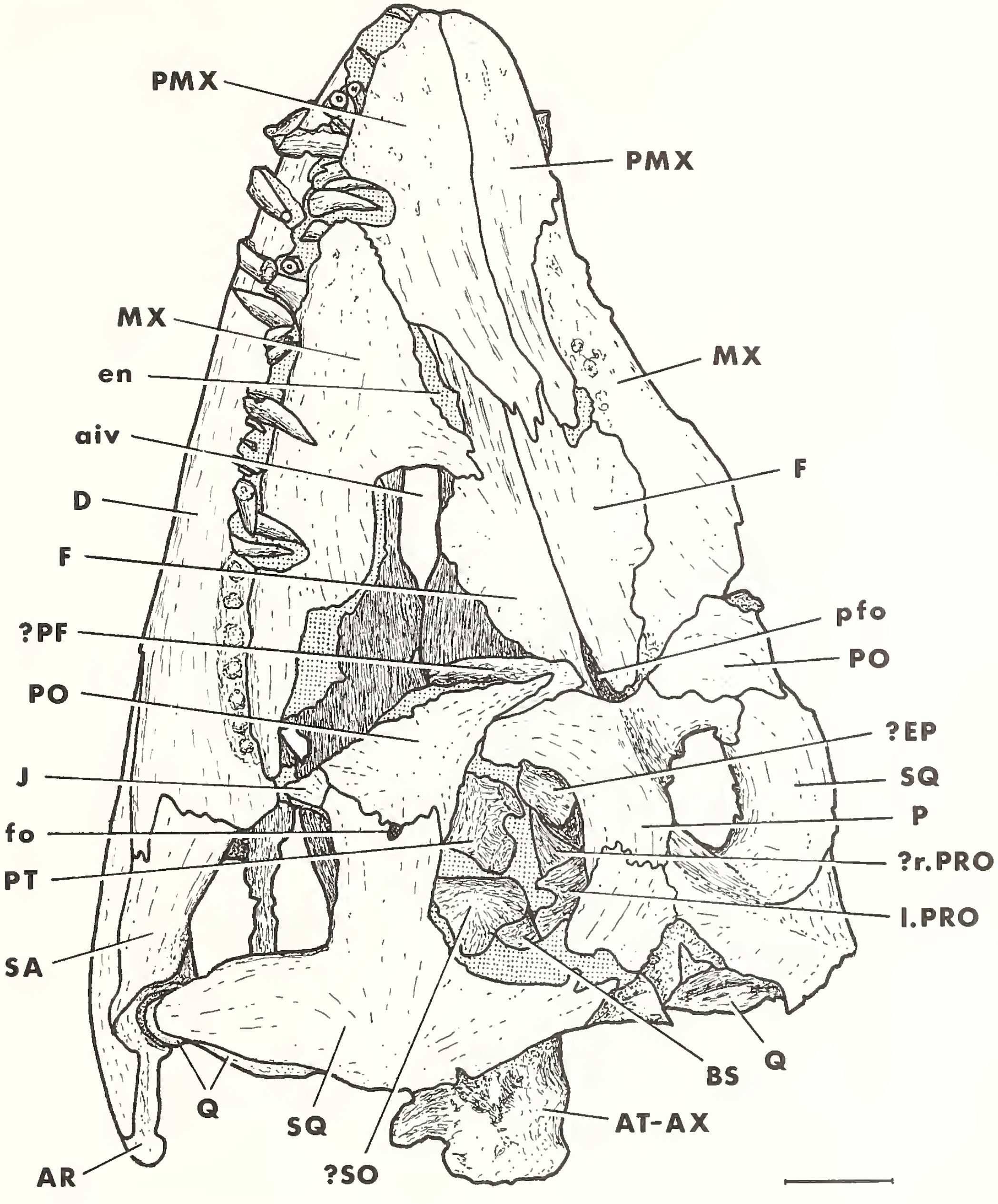
TEXT-FIG. 1. *Cryptoclidus eurymerus* (Phillips). PETMG R.283.412; dorsal view of skull; Dogsthorpe, near Peterborough, UK; Lower Oxford Clay (Callovian); ×0·5.

Diagnosis. See Brown (1981*b*, p. 255).

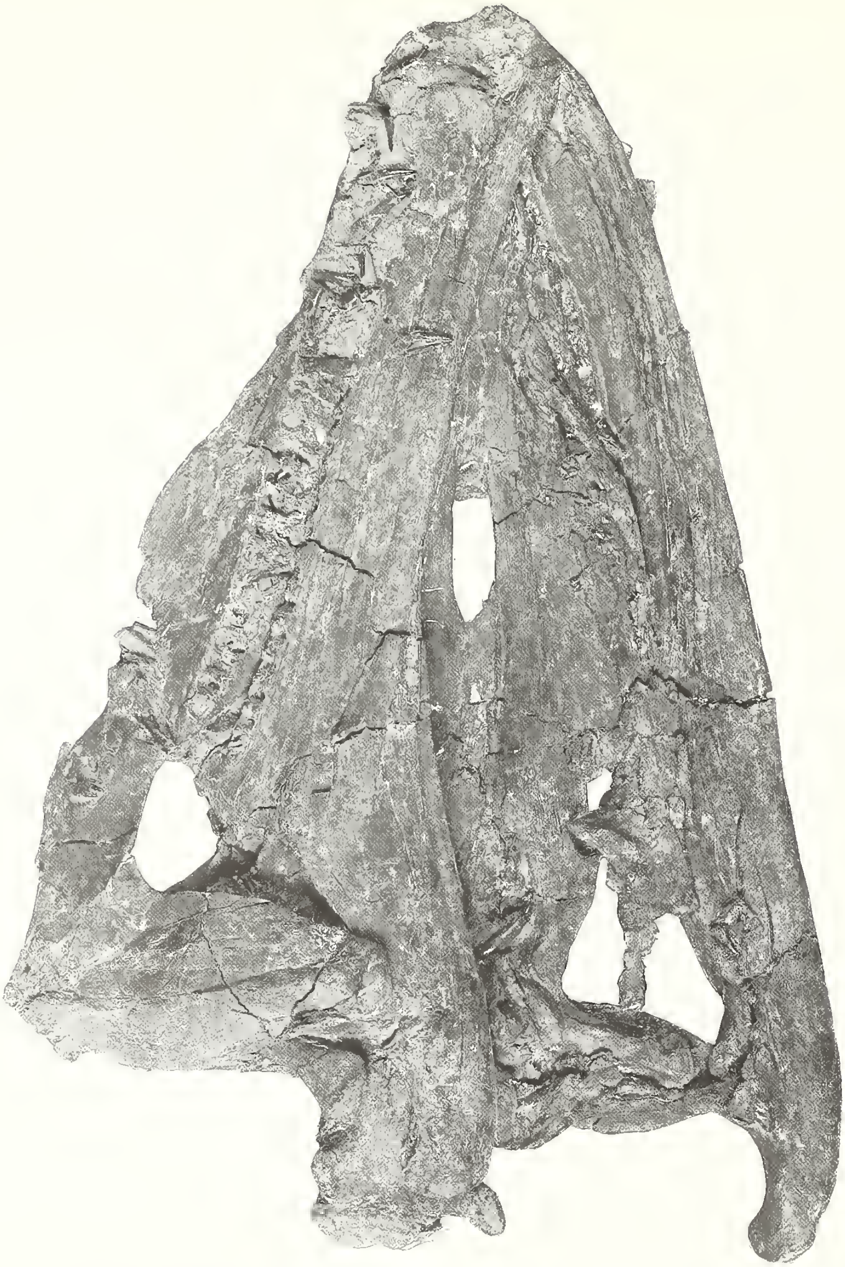
Cryptoclidus eurymerus (Phillips, 1871)

Text-figures 1–4

Synonymy. See Brown (1981*b*, p. 256).



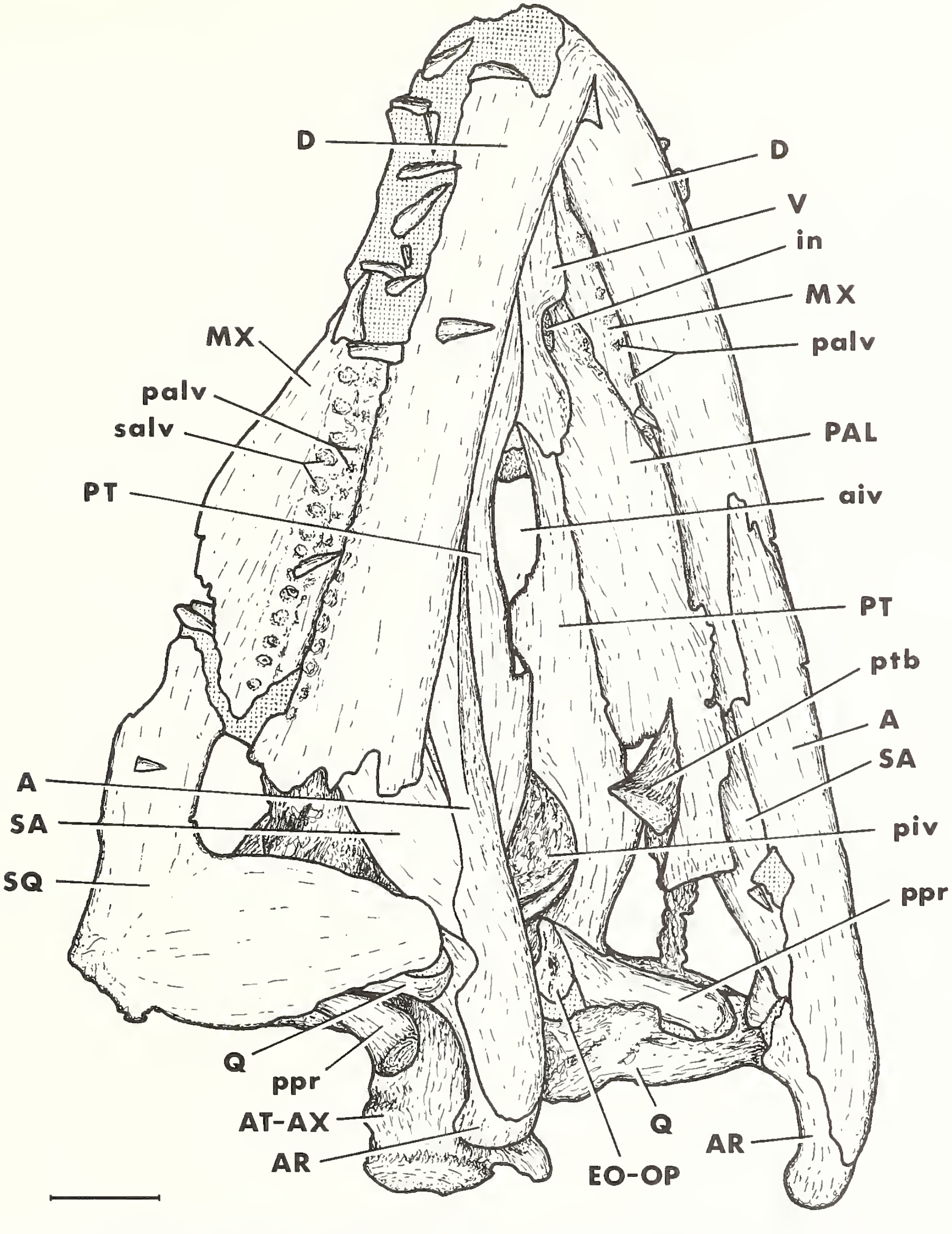
TEXT-FIG. 2. *Cryptoclidus eurymerus* (Phillips). Drawing of specimen in Text-figure 1, with residual matrix shown stippled. Abbreviations: A, angular; aiv, anterior interpterygoid vacuity; AR, articular; AT–AX, fused atlas–axis; BS, basisphenoid; D, dentary; en, external naris; EO–OP, fused exoccipital–opisthotic; EP, epipterygoid; F, frontal; fo, foramen; in, internal naris; J, jugal; L, lacrimal; l.PRO, left prootic; MX, maxilla; N, nasal; P, parietal; PAL, palatine; palv, primary alveoli; PF, postfrontal; pfo, pineal foramen; piv, posterior interpterygoid vacuity; PMX, premaxilla; PO, postorbital; ppr, paroccipital process of exoccipital–opisthotic; PRF, prefrontal; PT, pterygoid; ptb, pterygoid boss; Q, quadrate; QJ, quadratojugal; r.PRO, right prootic; SA, surangular; salv, secondary alveoli; SO, supraoccipital; SQ, squamosal; V, vomer. Scale bar represents 30 mm.



TEXT-FIG. 3. *Cryptoclidus eurymerus* (Phillips). PETMB R.283.412; palatal view of skull; Dogsthorpe, near Peterborough, UK; Lower Oxford Clay (Callovian); ×0·5.

Neotype. BMNH R2860, an almost complete adult skeleton from the Lower Oxford Clay of the Peterborough district (exact locality not known; see Andrews 1910, Brown 1981*b*). The fragmentary skull was hitherto the best specimen.

Diagnosis. See Brown 1981*b*, p. 255 (generic diagnosis: *Cryptoclidus*) and p. 257 (specific diagnosis).



TEXT-FIG. 4. *Cryptoclidus eurymerus* (Phillips). Drawing of specimen in Text-figure 3, with residual matrix shown stippled. Abbreviations as in Text-figure 2. Scale bar represents 30 mm.

Since the skull is known only for *C. eurymerus*, the cranial characters in both lists apply to the species.

Material. PETMG R.283.412 (accession number 307/1987), an almost complete skull and associated skeleton from Bed 10 of the Lower Oxford Clay, Dogsthorpe Brick Pit, near Peterborough (Grid Ref. TF 2130 0217).

Kosmoceras jason Zone (Calloman 1968; Martill 1985; Martill and Hudson 1991), Middle Jurassic, Callovian Stage.

DESCRIPTION

General features

As preserved, the flattened specimen includes also the atlas-axis complex. The skull is approximately 335 mm long and 225 mm at its widest. The general appearance is shown in Text-figures 1 and 3, and analysed in Text-figures 2 and 4. The skull has suffered some post-mortem crushing and disruption of the elements. The left side of the skull table lies over the palate, with the posterior dorsal surface of the palate visible through the disrupted left orbit. On the right side the skull table is broken at the level of the jugal bar and folded under onto the ventral aspect, so that the right orbit cannot be traced. The mandibles and palate are almost complete. Most of the endochondral braincase elements can be identified but are largely obscured by overlying membrane bones. New information provided by this specimen permits the lateral skull reconstruction of *C. eurymerus* given by Brown (1981*b*, text-fig. 1) to be redrawn (Text-fig. 5).

Skull roof

The specimen shows the entire dorsal midline and left cheek region (Text-figs 1–2), and provides new information on the structure of the external naris, orbital margins and postorbital bar.

The suture of the left premaxilla with the maxilla runs to the anterior corner of the external naris, but behind this the specimen shows the naris bordered medially by the frontal and laterally by the maxilla. Posteriorly, the premaxillae have been displaced to the right by about 10 mm revealing the underlying anterior parts of the frontals, which show strong anteroposterior ridging on the area of the squamous overlap. When this post mortem displacement is reversed, the premaxilla covers the frontal; it may even have met the maxilla at the posterior corner of the naris, thereby excluding the frontal from narial contact when seen in dorsal view. In Text-figure 5, the frontal is depicted making a small contact with the naris and narrowly separating premaxilla and maxilla at this point. The external naris is slit-like and 25 mm long by 5 mm wide at the front. Crushing has obscured the internal detail.

The left premaxilla shows the six tooth sockets characteristic for *Cryptoclidus*. The number of maxillary alveoli is estimated to be about twenty; it is not possible to count them on either side, the left upper toothrow being obscured posteriorly by the overlying dentary whilst the right is obscured anteriorly.

The frontals are abraded on the orbital margins, and thus the orbital outline cannot be restored with confidence. In the midline, the frontals continue back to meet the parietals and largely enclose the pineal foramen, the parietals contributing only about one quarter of its margin. The pineal foramen is deeply recessed into an embayment formed by diverging anterior wings of the parietals.

The parietals form the usual high and narrow sagittal crest. The squamosals cover the highest point of this crest at the back, and meet in the midline. This region of the specimen was exposed before collection and is abraded.

The bones of the cheek region are relatively well preserved, especially on the left side; and the postorbital is seen for the first time in *Cryptoclidus*. It is a triangular element, extends far down into the temporal fossa, and forms a significant part of its border. On its posterior margin it is overlapped by the squamosal: halfway along this margin the union is interrupted by a small foramen. The anterior margin of the left bone appears complete, and has a marked, crenulated edge for most of its length, indicating that this is the suture line for the postfrontal. Therefore the postorbital lay mostly below and behind the postfrontal, and may have had only a small exposure to the orbital margin.

The element tentatively identified here as the left postfrontal is largely overlain by the postorbital and itself overlies the suture between frontal and parietal. The outline of the orbit is badly distorted, and the structure and relationships of the postfrontal are unclear.

The jugal is represented on the left by a fragment of bone, which unites with the squamosal and postorbital, and forms part of the margin of the infratemporal fossa. Growth lines on the surface of this fragment indicate that the jugal was vertically orientated, and was probably a small and weak strap-shaped bone extending squamously over part of the postorbital anterior to the preserved part. A broken section through the end of the anterior process of the right squamosal shows the very thin and laminate squamosal overlying an equally thin jugal with, underlying these two elements, the relatively massive postorbital forming the chief mechanical component of this region. On neither side is any part of the posterior margin of the orbit preserved; nor is there any evidence for the nature of the union of the jugal with the maxilla.

The large squamosal has the usual sauropterygian triradiate structure, and overlies the outer surface of the massive quadrate.

Palate

The palate is largely undisturbed with the left side fully visible, and is here seen in *Cryptoclidus* for the first time. The general arrangement of the palatal bones (vomers, large palatines and pterygoids) appears to be as normal for plesiosaurs; but ectopterygoids cannot be identified and may be missing from the specimen. The pterygoids are separated by large anterior and posterior interpterygoid vacuities; posteriorly their relationship to the basis cranii and to the quadrates, both variable plesiosaurian characters, cannot be seen. There is no evidence for the existence of suborbital fenestrae; the lateral margins of the palatines are very thin and abraded but nevertheless intact, and the extent and continuity of abraded bone indicates strongly that they were absent.

The juxtaposition of the left internal and external nares can be observed on the specimen. The internal nares lie a few millimetres in advance of the external nares, the separation being greater on their posterior margins. Fine osteological details are not preserved.

Braincase

The disarticulated endochondral elements of the braincase are partly hidden dorsally by the bones of the skull roof and cheek, and in ventral view by the posterior part of the right mandibular ramus and the quadrate and squamosal. Both quadrates, fused exoccipital–opisthotic elements and the prootics together with the supraoccipital and the left epipterygoid may be identified (see Text-figs 2 and 4); but full description would be possible only by removing the overlying membrane bones and undertaking further preparation. The atlas and axis are preserved in articulation with the occiput.

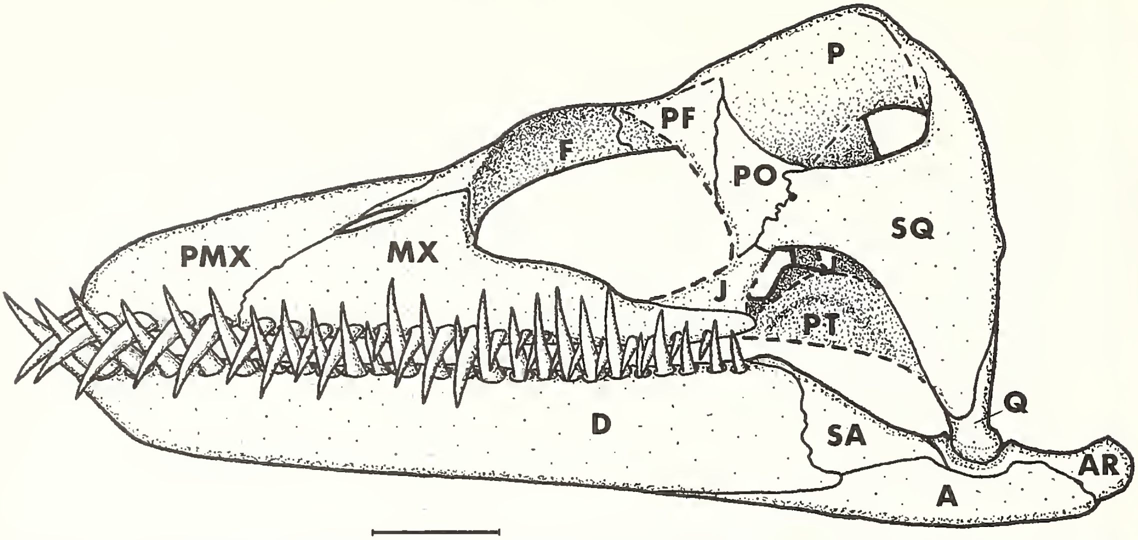
Mandibles

The right outer surface and left inner surface of the mandible are well displayed (Text-figs 3–4). The ventral edge of the left ramus is undisturbed and shows a straighter profile than previously reconstructed. Some post-mortem displacement has occurred between elements of the right ramus. There is no evidence for coronoid or prearticular elements, which seem to be absent in the species; neither is there any splenial, which to date has been identified only tentatively from fragments in a single skull (R8621; Brown 1981*b*, p. 264).

There are certainly twenty-six and possibly twenty-seven tooth positions. The dentition is represented by numerous teeth or tooth fragments both *in situ* and detached. The teeth show the characteristic reduced ornamental pattern diagnostic of *Cryptoclidus* (see Brown 1981*b*, fig. 5).

RECONSTRUCTION

The lateral skull restoration given by Brown (1981*b*, fig. 1) was based upon the fragmentary neotype skull (BMNH R2860) with the addition of tooth-row details from other specimens. Outlines of much of the snout including the external nares and the postorbital and jugal bars were conjectural. Specimen PETMG R.283.412 permits an objective restoration of the snout and external naris, adds details of the postorbital and jugal, and shows an undistorted mandibular profile. However, overall skull shape reconstruction cannot be improved. Text-figure 5 has been produced by modifying the 1981 restoration with respect to the above features of the new specimen. The orbital outline and the anterior extent of the postfrontal and jugal remain conjectural.



TEXT-FIG. 5. *Cryptoclidus eurymerus* (Phillips). Lateral restoration of skull after Brown (1981*a*, fig. 1), modified to show new osteological details from PETMG R.283.412. Scale bar represents 30 mm.

DISCUSSION

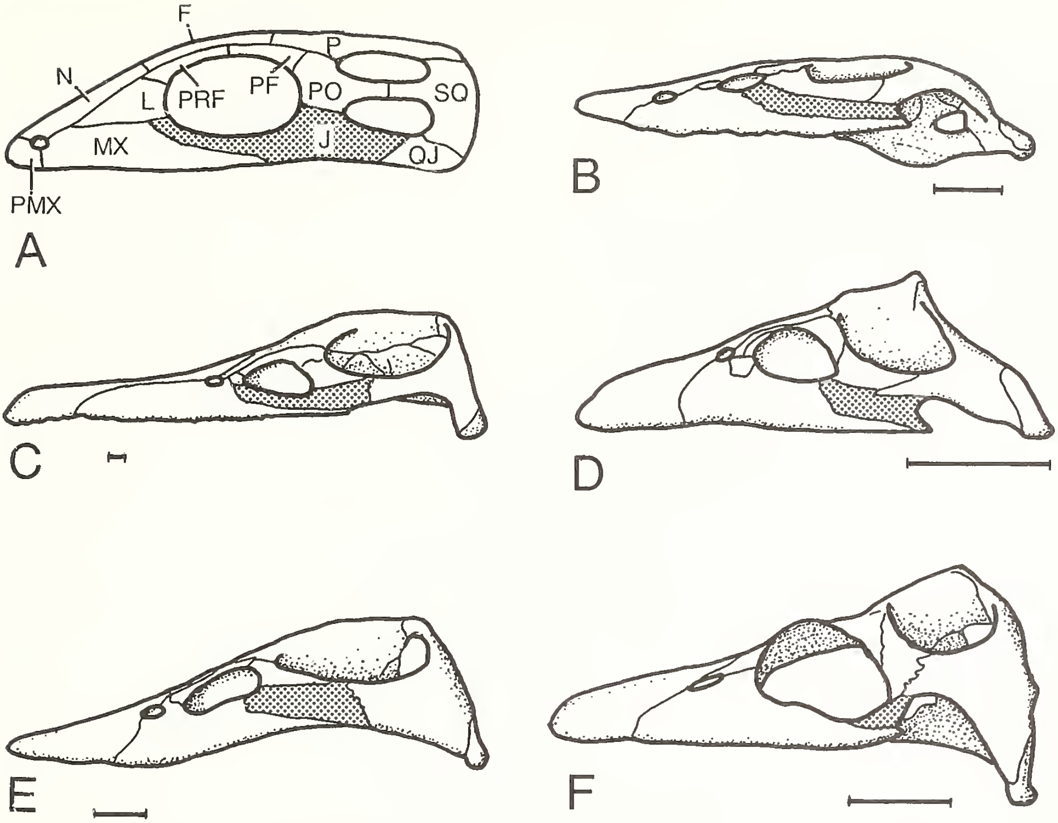
The cryptoclidid cheek

Brown (1981*b*, figs 1, 22, 29) reconstructed lateral views of the skulls of *Cryptoclidus*, *Tricleidus* and *Kimmerosaurus*, with the jugal shown as a narrow vertically orientated bar separating a large orbit from the infratemporal fossa. This pattern is at variance with reconstructions of Cretaceous elasmosaurid genera given by Welles (1949, 1952, 1962; see for example Text-fig. 6E), the restoration of the Upper Liassic species *Plesiosaurus guilelmiimperatoris* drawn by Fraas (1910, fig. 1), and the reconstruction of *Muraenosaurus* given by Andrews (1910, fig. 46b). In all of these the jugal is a large quadrilateral element, with a horizontal long axis, small borders on orbit and/or infratemporal fossa and a long suture dorsally with the postorbital. Brown's evidence for this configuration was inferred by the necessity to restore the anterior end of the squamosal in the best of the skulls which he reviewed (that of *Tricleidus*) in a position spatially well above the posterior end of the maxillary tooth row, and by the close resemblance of the form of the squamosal in *Cryptoclidus* and *Kimmerosaurus* to that of *Tricleidus*.

The first objective evidence supporting this cheek configuration in any plesiosaur was provided by Brown *et al.* (1986) for *Kimmerosaurus*. Chatterjee and Small (1989) described the new cryptoclidid genus *Turneria*, and in a tentative restoration (Chatterjee and Small 1989, fig. 2) showed a similar configuration. The new *Cryptoclidus* skull described above now provides objective evidence for the same cheek pattern in this genus also. Brown (1994) revised his classification of plesiosauroid families and genera; the 'vertically-orientated jugal bar separating orbital and infratemporal fossa margins' is made a diagnostic character of the family Cryptoclididae, and he includes *Tricleidus* (listed as an elasmosaurid in Brown 1981*b*) as a cryptoclidid genus.

Sauropterygian cheek and orbit evolution

Text-figure 6A shows the primitive diapsid cheek and orbital structure from which the various sauropterygian patterns (Text-fig. 6B–F) must be derived. The jugal is a large element of the circumorbital series linking the lacrimal to the postorbital, and thereby excluding the maxilla from the orbital margin. It meets the quadratojugal posteriorly and with it forms the lower temporal arch.



TEXT-FIG. 6. Representative sauropterygian skulls. Jugal shown stippled. Scale bar represents 50 mm. A, generalized primitive diaspid, redrawn from Romer (1966, fig. 155*d*). B, a nothosaurid (*Simosaurus*), redrawn from Storrs (1991, fig. 33*c*), after Huene (1921). C, a pliosaurid (*Pliosaurus brachyspondylus*), after Taylor and Cruickshank (1993, fig. 5). D, a plesiosaurid (*Plesiosaurus brachypterygius*), after Huene (1923, pl. 2, fig. 1). E, an elasmosaurid (*Styxosaurus snowii*), after Welles (1952, fig. 5). F, a cryptoclidid (*Cryptoclidus eurymerus*), reduction of Text-figure 3.

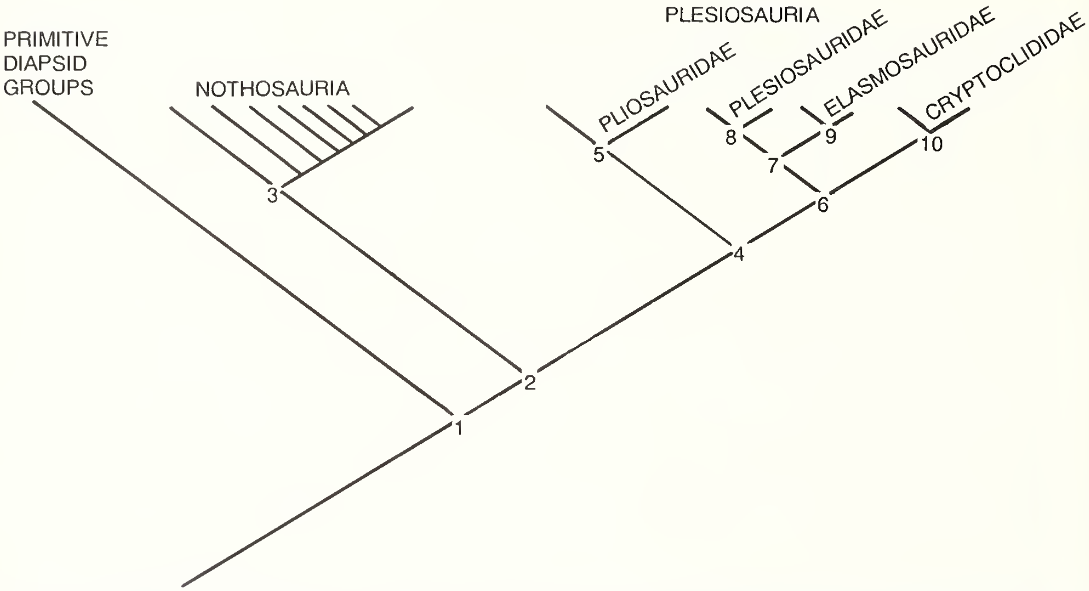
In the upper temporal arch the postorbital intervenes between the jugal and the anterior process of the squamosal.

In the Sauropterygia, the quadratojugal has been lost and the posterior part of the jugal remodelled. This results in absence of the lower temporal arch; but a deep ventral excavation of the lower cheek margin in nothosaurids, plesiosaurids and cryptoclidids (Text-fig. 6B, D, F) bears witness to the former presence of a lower temporal opening. Additionally, the anterior process of the squamosal has made contact with the jugal, excluding the postorbital from the new ventral cheek margin.

In the pliosaurid *Pliosaurus brachyspondylus* (Text-fig. 6C), the elongate jugal retains contact with the lacrimal anteriorly as in the diapsid ancestor (Taylor and Cruickshank 1993); and a similar contact of jugal and lacrimal, hidden from lateral view within the orbit, was described in the nothosaurid *Paranothosaurus* by Kuhn-Schnyder (1964) (see Storrs 1991, p. 144). In other nothosaurid and pliosaurid genera the jugal and lacrimal separate, and the lacrimal may be lost or more probably may be fused to the maxilla (as in *Rhomaleosaurus megacephalus*; Cruickshank 1994) resulting in a contact of the maxilla with the orbit.

In plesiosauroid genera the snout is shorter, the orbit is proportionally enlarged, the maxilla forms the major part of the lower orbital margin, and the jugal is shortened. In plesiosaurids and elasmosaurids (Text-fig. 6D, F), in which orbital enlargement is moderate, the jugal is quadrilateral with a horizontal axis. In cryptoclidids (Text-fig. 6E) there is a substantial increase in the relative size of the orbit, involving also a lateral rotation of the maxillary flange carrying the orbital margin outward (not clearly depicted in lateral restorations); and in addition the ventral cheek excavation is not only retained but possibly enlarged. The cryptoclidid jugal becomes elongated along its vertical axis so as to form a narrow bar separating the enlarged orbit from the margin of the infratemporal fossa.

The characters of the sauropterygian cheek and orbit are analysed phylogenetically in Text-figure 7. The inclusion of further character analysis is beyond the scope of the present work, and is largely dependent upon the results of an ongoing review of Lower Jurassic genera involving several workers. That review is almost certain to overthrow the present superfamily and family divisions of the Plesiosauria. Shared derived characters of cheek and orbit uniting the groups of the current classification are as follows.



TEXT-FIG. 7. Phylogenetic analysis showing interrelationships of major sauropterygian groups, based on characters of the cheek and orbit. Numbered nodes 1 to 10 are characterized in the text.

Node 1 (*outgroup: primitive diapsid*). Lower temporal bar present. Jugal contacts lacrimal anteriorly and is separated from squamosal by postorbital.

Node 2 (*Sauropterygia*). Loss of quadratojugal breaks lower temporal arch; a deep ventral excavation of the lower cheek margin results, and quadrate becomes visible laterally. Jugal contacts squamosal.

Node 3 (*Nothosauria*). Contact between jugal and lacrimal retained within orbit in some; contact lost in others, with maxilla intervening.

Node 4 (*Plesiosauria*). Cheek/orbit characters as in Node 2.

Node 5 (*Pliosauroidea, Pliosauridae*). Progressive reduction in ventral cheek excavation. Contact between jugal and lacrimal retained and visible laterally in some; contact lost in others, with maxilla intervening.

Node 6 (*Plesiosauroidea*). Snout shorter than at Node 2, with proportionally larger orbit. Contact of jugal and lacrimal lost, maxilla intervenes and forms the major part of the lower orbital margin.

Jugal quadrilateral with horizontal long axis and short contacts on orbital and ventral cheek margins.

Nodes 7 and 8 (*Plesiosauridae*). Cheek/orbit characters as in Node 6.

Node 9 (*Elasmosauridae*). Reduction of ventral cheek excavation.

Node 10 (*Cryptoclididae*). Orbit proportionally larger than in Node 6. Deep ventral excavation of cheek margin retained and perhaps increased. Jugal reduced to a narrow vertically-orientated bar separating orbit from ventral cheek margin.

Using characters only of the cheek and orbit, it would be equally parsimonious to link Nothosauria and Pliosauridae as a sister group of the Plesiosauroidea. In preparing Text-figure 7 we have borne in mind many other characters, such as those associated with marine adaptation of the postcranial skeleton, which firmly unite the Pliosauridae with the Plesiosauroidea.

Olfactory system

Cruickshank *et al.* (1991) and Cruickshank (1994) described the structure of the internal and external nares in *Rhomaleosaurus megacephalus* (Stutchbury), and concluded that this pliosaurid possessed a unique system of underwater olfaction. Water entered the mouth at or near the premaxilla–maxilla suture, and then passed to the anteriorly-placed internal nares. It was then sucked over the olfactory epithelium and out of the more posteriorly-placed external nares by hydrodynamic forces generated by the forward movement of the animal. The internal nares in *Cryptoclidus* are anteriorly placed with respect to the external nares as in *Rhomaleosaurus*, and on that basis a similar mechanism may be invoked for *Cryptoclidus*. Use of this mechanism seems to be a constant feature of the Plesiosauria (Taylor and Cruickshank 1993; Cruickshank 1994).

Jaws and feeding habit

By comparison with pliosauroid skulls, such as that of *Rhomaleosaurus zetlandicus* (Phillips) (see Taylor 1992), the skull of *Cryptoclidus eurymerus* is more lightly built. It lacks structures such as the large pterygoid flange; the suborbital fenestra (site of insertion of an enlarged anterior pterygoideus muscle); thick very strong teeth, and construction of the lower jaw as a stout beam resistant to substantial torsional loads; all of which Taylor (1992) explained in terms of a twist-feeding predatory habit in *Rhomaleosaurus*. Clearly *Cryptoclidus* did not feed in this way. The increased number and decreased size of the teeth by comparison with plesiosaurids and elasmosaurids is not as marked in this genus as in more advanced cryptoclidid genera such as *Kimmerosaurus* Brown; but it seems likely that the prey was nevertheless small and relatively soft, perhaps including soft-bodied cephalopods and small fishes. The general structure is compatible with a filter-feeding habit suggested for cryptoclidids by Brown (1981*a*), and resembles that of modern 'krill' feeders described by Massare (1987). The mandible in *Cryptoclidus eurymerus* lacks the prearticular and the coronoid. Both these elements are present in primitive pliosauroids (Taylor 1992; Cruickshank 1994), and *Tricleidus* Andrews (now included in the Cryptoclididae as a primitive genus: Brown 1994) retains a much-reduced coronoid (Andrews 1910) but has lost the prearticular. It would appear that the prearticular and coronoid help to brace the dentary to the postdentary bones, since in pliosaurs (and also in the one skull of *Tricleidus*) the mandible is invariably preserved as a single structure; whereas in *Cryptoclidus* (present paper; Brown 1981*b*) and *Kimmerosaurus* (Brown 1981*b*; Brown *et al.* 1986) it is usual to find the dentary displaced with respect to the postdentary elements. This feature of preservation further demonstrates the difference in torsional strength related to differing feeding habits between pliosauroids and cryptoclidids.

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